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TWO NEW VARIETIES OF *ERIOGONUM OVALIFOLIUM* (POLYGONACEAE) FROM THE INTERMOUNTAIN WEST, USA

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ABSTRACT

Two long-known varieties of *Eriogonum ovalifolium*, **E. ovalifolium** var. **focarium** Reveal & Mansfield, **var. nov.**, and E. **ovalifolium** var. **rubidium** (Gand.) Reveal & Mansfield, **comb. nov.**, are proposed. The first is confined to the volcanic cinders flats and slopes of Craters of the Moon National Monument, Butte County, Idaho, and related to the more widespread, northern, higher elevation var. *depressum*. The second variety is restricted to Steens Mountain of Harney County, Oregon; it is allied to var. *nivale* of the Sierra Nevada/Cascade cordillera. A key to the varieties is provided.

In our respective floristic work we have long known about two curious expressions of *Eriogonum ovalifolium* Nutt. (Polygonaceae Juss; *Eriogoneae* Dumort.), one at the Craters of the Moon National Monument in Butte County, Idaho, and a second from the higher elevations of Steens Mountain in Harney County, Oregon. Reveal (2012) acknowledged that the former was easy to distinguish from var. *depressum* Blank. because of its bright white tomentum and lower elevation habitat, but the second was much more difficult, and in frustration he assigned the Steens Mountain plant to var. *depressum* after long determining specimens of this entity as var. *nivale* (Canby ex Coville) M.E. Jones. Mansfield (2000), in his *Flora of the Steens Mountains*, properly assigned the later to var. *nivale* as then understood, and indeed that is a far more exact association than that suggested by Reveal in *Intermountain Flora*.

In 2012, as part of the annual meeting of The Eriogonum Society, we were both on Steens Mountain and were able to carefully examine the plant and determined that it was readily distinguished from var. *nivale* of the Sierra Nevada/Cascade cordillera by its prostrate to decumbent scapes. Deciding that it was time to describe this expression, plans were made to study the plant at Crater of the Moon in 2013. This was done in July by Mansfield with permission of the Park Service.

Eriogonum ovalifolium Nutt. var. **focarium** Reveal & Mansfield, **var. nov.** **Type. USA. Idaho.** Butte Co.: Craters of the Moon National Monument, 15 Jul 1941, *A. Cronquist 2395* (holotype: UTC; isotypes: IDS, MO). Figures 1 and 2.

Distinguished from var. *depressum* by the bright white lanate pubescence of the leaves

Plants 0.5–3 dm across; **leaf blades** usually round, 0.2–0.8 cm long, brilliantly white lanate, the margins not brownish; **scapes** mostly erect, 0.3–5(–8) cm long, mostly lanate; **inflorescences** capitate, 1–2.5 cm wide; **involucres** 4–8 per cluster, (2.5–)3–4 mm long; **flowers** 4–5 mm long, the perianth cream to pale yellow, becoming yellowish-red to rose in fruit.

Flowering May-Aug. Black volcanic gravel on gentle slopes and flats in sagebrush communities, conifer woodlands, 1600–1900 m; endemic to Craters of the Moon National Monument, Butte Co., Idaho.

Representative specimens: **USA. IDAHO.** Butte Co.: Craters of the Moon: 20 Jun 1930, *Applegate 6337* (DS), 13 May 1940, *Barkley 5073* (MONTU), 25 Jul 1932, *Christ 1930* (NY), 14 Aug 1937, *Eggler & Eggler 198* (MIN), 2 Jul 2013, *Mansfield et al. 13-223* (CMNP), 22 Jun 1962, *McElroy & Hambly s.n.* (UT), 22 Jun 1938, *Weaver 38-105* (WIS).

Craters-of-the-Moon wild buckwheat, *Eriogonum ovalifolium* var. *focarium* (Latin *focarius*, of the oven, as to the habitat), is restricted to black volcanic cinders flats and slopes that dominate the Craters of the Moon National Monument, a formation that has evolved via a series of eight eruptions over the past 15,000 years, the most recent about 2000 years ago. Given that these events occurred at the end of the last ice age, it is likely that populations of *E. ovalifolium*, and most likely the var. *depressum* phase, occupied the newly created site. With the onset of the hypsithermal, and the pronounced warming of the climate, those individuals able to adapted to the volcanic soil and high temperatures, likely evolve so that today the var. *focarium* is found some 2000 feet below populations of var. *depressum* found on the nearby mountains just to the north. Likewise, the intense sunlight and ground heat of the black gravel probably promoted the survival of plants with dense, brilliantly white lanate to tomentose pubescence that evolved as a mechanism to reflect both light and heat.

Figure 1. Habit of *Eriogonum ovalifolium* var. *focarium*.

Figure 2 Mature flowers (above) and leaves of *Eriogonum ovalifolium* var *focarium*.

Figure 3. Habit of *Eriogonum ovalifolium* var. *rubidium*.

Figure 4. Prostrate scapes (above) and flowers with achenes of *Eriogonum ovalifolium* var *rubidium*.

Eriogonum ovalifolium Nutt. var. **rubidum** (Gand.) Reveal & Mansfield, **comb. nov.** *Eriogonum rubidum* Gand., Bull. Soc. Roy. Bot. Belgique 42: 194. 1906. **TYPE. USA. Oregon.** Harney Co.: Head of Wild Horse Creek, Steens Mountain, 15 Jul 1898, *W.C. Cusick 2039* (holotype: LY; isotypes: E, F, G, GH, K, MIN, MO, MSC, NDG(3), P, POM, ORE, UC, US). Figures 3 and 4.

Plants 0.5–5(–7) dm wide; **leaf blades** broadly ovate to round, 0.5–1.2 cm long, densely greenish white-tomentose, the margins occasionally brownish; **scapes** decumbent to prostrate, 0.3–5 cm long, mostly tomentose; **inflorescences** capitate, 1–2.5 cm wide, the branches absent; ***involucres*** 4–8 per cluster, 3–4.5 mm long; **flowers** 4–5 mm long, the perianth white to rose or red.

Flowering Jun-Sep. Sandy to gravelly often worn volcanic slopes and ridges in mixed grassland and sagebrush communities; 2700–3000 m; endemic to Steens Mountain, Harney Co., Oregon.

Representative specimens. **USA. OREGON.** Harney Co.: Steens Mountain: Head of Little Blitzen Gorge, 19 Aug 1971, *Chambers 3342* (NY, OSC, UTC); Alvord Creek, 30 Jun 1959, *Cronquist 8581* (NY, TEX, UTC; N of Wildhorse Lake, 17 Jul 1979, *Ertter & Strachan 3119* (MARY, NY, UTC); rim above Mosquito Creek, 28 Jul 1976, *Grimes 1009* (CIC); rim above Mosquito Creek, 3 Oct 1976, *Kotter 76-208* (CIC); head of Little Blitzen River, 15 Jul 1966, *Holmgren & Reveal* 2880 (BRY, CAS, DS, IDS, KSC, MARY, MIN, MO, MSC, NY, OKL, OKLA, RM, RSA, TEX, UT, UTC); head of Blitzen Canyon, 1 Aug 1946, *Maguire & Holmgren 26809* (CAS, DS, NY, TEX, UC, UTC); above Blitzen Gorge, 16 Jul 1935, *Thompson 12110* (DKL, CAS, DS, MO, MONTU, NY, POM, WTU).

The distinctiveness of the Steens Mountain wild buckwheat, var. *rubidum* (Steens Mountain, Harney County, Oregon, the type location; named for Major Enoch Steen, a U.S. Army officer, in 1860), is not immediately obvious when examining herbarium specimens, but is so when seen in the field because instead of the upright, albeit short, scapes of var. *nivale*, those of var. *rubidum* are typically prostrate. Likewise, the color of the leaf tomentum, being greenish white is different from the typically bright white of the leaves of var. *nivale*. It is suggested that the Steens Mountain expression is the result of isolation and local selection to avoid the brisk and often persistent winds whipping across the summit of the mountain. As the variety also occurs in low sagebrush environments and in an area of heavy winter snows, another factor might be its reduction in stature by only a few centimeters to decrease the impact not only of the wind but also to reduce herbivory. The leaf tomentum is not as white var. *nivale* and thus approaching that of var. *depressum*, but the color pattern of the flowers point to a closer evolutionary history with var. *nivale* than var. *depressum* as does the tendency of most individuals to have a brown tinge to the margin of the leaf blade so typical of the western variant.

Key to the varieties of *Eriogonum ovalifolium*

1. Leaf blades 0.2–1.2 (–2) cm long; scapes usually 0.3–5 (–9) cm long, rarely longer; involucres usually 2–4.5 (rarely 5–8) mm long.

2. Perianth yellow; c Nevada and ec California ..... 1. var. **caelestinum**
2. Perianth white, sometimes rose, purple, or red; widespread.

3. Leaf margins brownish.

4. Leaf blades densely lanate, the margins consistently brownish ..... 2. var. **eximium**
4. Leaf blades tomentose, usually without a brownish margin ..... 3. var. **williamsiae**

3. Leaf margins not brownish or, if so, plants of high elevation, c Sierra Nevada and se Oregon.

5. Involucres 5–8 mm long.

6. Leaf blades white-lanate; San Bernardino Mountains, s California ..... 4. var. **vineum**
6. Leaf blades tomentose to floccose; s Sierra Nevada, California ... 5. var. **monarchense**

5. Involucres 3–4.5 mm long.

7. Leaf blades greenish and thinly tomentose at least adaxially, usually elliptic, infrequently oblong to spatulate; scapes often suberect to decumbent, usually thinly floccose; Rocky Mountains of Alberta, Idaho, Montana, and Wyoming, and ne Oregon .... 6. var. **depressum**
7. Leaves densely lanate to white-tomentose on both surfaces or only slightly less so adaxially, not at all greenish, usually round; scapes prostrate to erect, lanate or tomentose; Sierra-Cascade cordillera, desert ranges of Great Basin, and Craters of the Moon National Park, Idaho.

8. Scapes prostrate; flowers bright white at anthesis, pink to purplish-red or deep red in fruit; Steens Mountain, Oregon ..... 7. var. **rubidium**
8. Scapes decumbent to erect; flowers bright white at anthesis to pinkish in fruit, or yellowish white to pale pinkish in fruit; Sierra-Cascade cordillera, disjunct at Craters of the Moon National Park, Idaho.

9. Scapes mostly decumbent; flowers bright white at anthesis to pinkish in fruit; Sierra-Cascade cordillera ..... 8. var. **nivale**
9. Scapes erect or nearly so; flowers yellowish white at anthesis, pale pinkish in fruit; Craters of the Moon National Park, Idaho ..... 9. var. **focarium**

1. Leaf blades usually 1–6 cm long, occasionally shorter; scapes (1–) 5–30 (–40) cm long; involucres (3.5–) 4–6.5 (–8) mm long.

10. Scapes usually 1–5 (–7.5) cm long; leaf margins brownish; rare, wc Nevada, ec California.

11. Leaf blades densely lanate, the margins brownish ..... 2. var. **eximium**
11. Leaf blades white-tomentose, the margins nearly always not brownish . 3. var. **williamsiae**

10. Scapes usually (4–) 7–30 (–40) cm long, rarely shorter; leaf margins only rarely brownish; widespread.

12. Inflorescences umbellate, branches 1–3 cm long; c Idaho and Montana .... 10. var. **pansum**
12. Inflorescences capitate, branches absent; widespread.

13. Flowers 5–7 mm long; involucres 5–7 mm long; s California ..... 4. var. **vineum**
13. Flowers 4–5 mm long; involucres 4–6.5 mm long; widespread.

14. Perianth yellow ..... 11. var. **ovalifolium**
14. Perianth white to rose or purple.

15. Leaf blades spatulate, oblong, or obovate to oval; scapes (4–) 5–20 cm long; widespread ..... 12. var. **purpureum**
15. Leaf blades oblanceolate to narrowly elliptic; scapes (15–) 20–30 (40) cm long; Montana and Wyoming ..... 13. var. **ochroleucum**

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TWO NEW VARIETIES OF *ERIOGONUM WRIGHTII* (POLYGONACEAE) FROM BAJA CALIFORNIA, MEXICO

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ABSTRACT

Two shrubby members of *Eriogonum wrightii*, **E. wrightii** var. **brevifolium** Reveal, **var. nov.**, and E. **wrightii** var. **linearifolium** Reveal, **var. nov.**, both long-known but heretofore not validly published, are proposed. The first is confined to the mountains of eastern Baja California from Sierra San Borgas and Sierra San Lucas south to Volcán las Tres Vírgenes. The second variety is restricted to Isla de la Guarda in the Sea of Cortez.

Two shrubby expressions of *Eriogonum* Michx. (Polygonaceae Juss.: Eriogoneae Dumort.) were collected in the early 1960s by the late Reid V. Moran (1916–2010) of the San Diego Museum of Natural History and the foremost botanical collector of the Baja California flora for nearly half a century. Known for his wit and his fine collections, Reid was greatly admired by many for his skill as a critical monographer, especially of Crassulaceae, and for his willingness to venture into remote and rarely visited areas of Mexico in search of plants. Over the subsequent years attempts were made to recollect both entities but as is often the case with rare plants in Baja, getting there at exactly the right moment is often not possible. Thus, after knowing of these expressions for some thirty years, and having collected, with Reid, small samples of one, these varieties are presented now so that the names might be used in on-going floristic studies.

Eriogonum wrightii Torr. ex Benth. var. **brevifolium** Reveal, **var. nov. TYPE. MEXICO. Baja California Norte.** San Juan Mine, Sierra San Borja, 23 Mar 1960, *R.V. Moran 7891* (holotype: SD; isotypes: DS, RSA, UC).

Allied with *Eriogonum wrightii* var. *pringlei* (J.M. Coult. & Fisher) Reveal of southwestern Arizona and northwestern Sonora, Mexico, but differing in having elliptic leaf blades 0.3–0.7 cm long and 0.1–0.25 (0.4) cm wide (not oblanceolate to narrowly elliptic, 0.7–1.5 cm long, 0.2–0.5 cm wide) and by having involucres 2–2.5 mm long (not 1–1.5 mm long).

Plants shrubs, 3–6 dm tall, 4–8 dm across; ***aerial flowering stems*** lanate; ***leaves*** with petiole bases not forming distinct ring around stem, the blades elliptic, 0.3–0.7 cm long, 0.1–0.25 (0.4) cm wide; ***inflorescences*** dense, the branches somewhat stout; ***involucres*** 1–1.5 mm long; ***flowers*** 1.5–2 mm long, the perianth white to pink; ***achenes*** 2–2.5 mm long.

Other specimens seen. **MEXICO. Baja California Sur.** Above El Terminal, 25 Nov 1961, *Moran 8512* (DS, RSA, SD, UC, US); below El Alamoso, 24 Dec 1963, *Moran 11410* (DS, RSA, SD, UC, US); Cerro la Sandía, 24 Jan 1964, *Moran 11538* (DS, SD); Cataviñcito, 21 Nov 1976, *Moran 23809* (SD, US); N slope of Volcán las Tres Vírgenes, 18 Feb 1973, *Moran & Reveal 20194* (SD, US); Volcán las Tres Vírgenes, 18 Feb 1973, *Moran & Reveal 20212* (MEXU, SD); 2 miles N of Yubay, 23 Feb 1973, *Moran & Reveal 20240* (SD).

The var. *brevifolium* (Latin *brevis*, short, and *folius*, leaf, as to the comparative length of the leaf compared to var. *linearifolium*) may be quickly distinguished by its whitish lanate aerial stems and inflorescence branches, and its short but broad leaf blades. The plant is found in gravelly to rocky soils in desert scrub at 700–1600 m from the Sierra San Borgas and Sierra San Lucas south to Volcán las Tres Vírgenes, Baja California, Mexico.

Eriogonum wrightii Torr. ex Benth. var. **linearifolium** Reveal, **var. nov.** TYPE. **MEXICO. Baja California Norte**. 4 mi SE of Refugio Bay, Isla de la Guarda, 22 Mar 1963, *R.V. Moran 10480* (holotype: SD; isotypes: DS, RSA, UC).

Allied with *Eriogonum wrightii* var. *pringlei* (J.M. Coult & Fisher) Reveal of southwestern Arizona and northwestern Sonora, Mexico, but differing in having linear to linear-oblanceolate leaf blades, 0.1–0.2 cm wide (not oblanceolate to narrowly elliptic and 0.2–0.5 cm wide) and by having involucres 1.5–2 mm long (not 1–1.5 mm long).

Plants shrubs, 4–8 dm tall, 5–10 (12) dm across; ***aerial flowering stems*** lanate; ***leaves*** with petiole bases not forming distinct ring around stem, the blades linear to linear-oblanceolate, 0.7–1.8 cm long, 0.1–0.2 cm wide; ***inflorescences*** dense, the branches slender; ***involucres*** 1.5–2 mm long; ***flowers*** 1.5–2 mm long, the perianth white to pink or rose; ***achenes*** 1.5–2 mm long.

Other specimens seen. **MEXICO. Baja California Norte**. W of Punta Diablo, Isla de la Guarda, 24 Mar 1959, *Moran 7235* (DS, SD – not in flower).

The var. *linearifolium* (Latin *linearis*, line, linear, and *folius*, leaf, as to the narrow leaf-blade) is readily distinguished from other expressions of the species by its long, narrow leaf blades and its isolated as well as southernmost distribution. It is known only the Isla de la Guarda in the Sea of Cortez.

A key to the varieties of *Eriogonum wrightii* is presented below.

1. Plants loosely to compactly matted herbs.

2. Plants 0.1–0.3 (–0.6) dm tall; leaf blades 0.1–0.25 cm long; involucres 0.8–1.7 (2) mm long; se California ..... 11. var. ***olanchense***
2. Plants 0.5–2.5 (–3) dm tall; leaf blades 0.3–1.2 cm long; involucres 1.5–4 mm long; e and s California, wc Nevada and n Baja California.

3. Inflorescences virgate or cymose; flowers 2–3 mm long; California and Nevada ..... 10. var. ***subscaposum***
3. Inflorescences capitate or nearly so; flowers 3–4.5 mm long; Sierra Juárez and Sierra San Pedro Mártir Baja California ..... 12. var. ***oresbium***

1. Plants shrubs or subshrubs.

4. Flowering stems and branches grayish or whitish lanate to densely tomentose; sw Arizona, se California and nw Mexico.

5. Leaf blades linear to linear-oblanceolate, 0.1–0.2 cm wide; Isla Angel de la Guarda, Baja California ..... 8. var. ***linearifolium***
5. Leaf blades oblanceolate to narrowly elliptic, 0.25–0.9 cm wide; sw United States and nw Mexico.

6. Flowers 3–4 mm long; involucres 1.5–2.5 mm long; achenes 2–3 mm long; plants usually sparsely branched; se California, sw Arizona, ne Baja California ..... 5. var. ***nodosum***
6. Flowers 1–2 mm long; involucres 0.7–1.5 mm long; achenes 1–2.5 mm long; plants usually densely branched; sw Arizona and Sonora, Mexico and in ec Baja California.

7. Leaf blade oblanceolate to narrowly elliptic, 0.7–1.5 cm long, 0.2–0.5 cm wide; involucres 1–1.5 mm long; sw Arizona and Sonora, Mexico ..... 6. var. ***pringlei***
7. Leaf blade elliptic, 0.3–0.7 cm long, 0.1–0.25 (–0.4) cm wide; involucres 2–2.5 mm long; Sierra San Borgas and Sierra San Lucas s to Volcán las Tres Vírgenes, Baja California, Mexico ..... 7. var. ***brevifolium***

4. Flowering stems and branches reddish or greenish tomentose to floccose or subglabrous; widespread.

8. Plants low and prostrate; inflorescences with racemosely arranged involucres; aerial stems and branches floccose to subglabrous; Isla Cedros, n Baja California ..... 3. var. ***taxifolium***
8. Plants distinctly shrubby or if low and spreading then plants not of Isla Cedros.

9. Petiole bases forming distinct ring around stem; leaf blades 0.2–0.6 (–1) cm long, 0.1–0.3 (–0.4) cm wide; s California and n Baja California ..... 4. var. ***membranaceum***
9. Petiole bases not forming distinct ring around stem; leaf blades 0.5–3 cm long, 0.2–1 cm wide; sw United States and Mexico.

10. Leaf blade 0.5–1.5 cm long, 0.2–0.5 (–0.7) cm wide; involucres 2–3 mm long; flowers 3–4 mm long; coastal bluffs n of Ensenada, Baja California, Mexico ..... 2. var. ***dentatum***
10. Leaf blade 0.5–3 cm long, 0.2–1 cm wide; involucres 2–2.5 or 3–4 mm long; flowers 2.5–4 mm long; California to w Texas s to c Mexico.

11. Leaf blades 0.5–1.5 cm long, 0.2–0.5 (–0.7) cm wide; involucres 2–2.5 mm long; flowers 2.5–3.5 mm long; se California to w Texas s to c Mexico ..... 1. var. ***wrightii***
11. Leaf blades 1.5–3 cm long, 0.5–1 cm wide; involucres 3–4 mm long; flowers 3–4 mm long; c and nw California ..... 9. var. ***trachygonum***

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I could fill the rest of the page with acknowledgements, but as Reid has already done this in his famous "I got it there, then" paper in Madroño, I will simply say thank you Reid, you are greatly missed.

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ERIOGONUM ×AMMEI (POLYGONACEAE), A NEW GARDEN HYBRID

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ABSTRACT

An unusual hybrid seedling involving California's insular endemic *Eriogonum arborescens* and a shrub common to the Mojave Desert, *E. fasciculatum* var. *polifolium*, was discovered in a California nursery, which grew rapidly to form a low, spreading shrub up to 1 m high and 3.5 m across with large, cymose, densely flowered inflorescences bearing white, slightly pubescent flowers. The new hybrid is named here as **Eriogonum ×ammei** Reveal & Veilleux, **hybid. nov.**

Hybrid populations involving insular and coastal species of *Eriogonum* Michx. (Polygonaceae Juss.: *Eriogoneae* Dumort.) are occasionally encountered along the coast of California as a result of the unfortunately widespread use of *E. giganteum* S. Watson and, to a lesser extent, *E. arborescens* Greene, in roadside plantings by the California Department of Transportation (Caltrans). As a result, hybrid populations involving St. Catherine's-Lace, *E. giganteum* var. *giganteum*, and coastal populations of *E. fasciculatum* Benth. (California buckwheat), and *E. cinereum* Benth. (coastal wild buckwheat), are found where these entities are in close proximity. A garden hybrid involving the two insular species, *E. arborescens* and *E. giganteum*, was known for many years before named *E. ×blissianum* by Herbert Mason in 1938. The latter is still widely planted mainly as a decorative plant around homes and in parks.

The discovery of another garden hybrid, especially one that grows to a large size in a matter of months, and is even more decorative than *Eriogonum ×blissianum*, means that the hybrid has the potential of being an important new introduction into the California garden flora.

Eriogonum ×ammei Reveal & Veilleux, **hybid. nov.** **TYPE. USA. California**. Alameda Co.: East Bay Wilds Native Plant Nursery, 28th Avenue at Foothill Boulevard, Oakland, 8 Oct 2013, *P. Veilleux s.n.* (holotype: BH). Figures 1–3.

The East Bay wild buckwheat, *Eriogonum ×ammei*, differs from its maternal parent, *E. arborescens*, by its fasculate leaves and broad leaf blades 0.3–0.8 (–1) cm wide (not solitary and 0.1–0.4(–0.6) cm wide) and from the paternal parent by the large, cymose inflorescence (not capitate to cymose-umbellate or rarely cymose), the cinereous lower surface of the leaf blade (not canescent or tomentose), and from both parents by its low, spreading habit and ability to grow to a large size so rapidly.

Plants low, spreading, fast-growing shrubs, 5–10 dm tall, 20–35 dm across, sparsely canescent; ***stems*** spreading, without persistent leaf bases, up to 1/2 height of plant, the aerial

flowering stems slender, solid, not fistulose, 0.5–1 (2) dm long, sparsely canescent; ***leaves*** cauline, fasciculate, the petioles 0.1–0.2 cm long, tomentose, the blades mostly narrowly elliptic, 0.5–3.5 cm long, 0.3–0.8 (1) cm wide, densely white cinereous (except for midvein and lateral veins) abaxially, dark green and essentially glabrous adaxially, the margins plane; ***inflorescences*** cymose, 2–3.5 dm tall, 2–5.5 dm across, sparsely canescent, ***peduncles*** absent, ***involucres*** solitary but in tight, congested clusters, turbinate to turbinate-campanulate, 3–4 mm long, 2–3.5 mm wide, sparsely canescent, the teeth 5, erect, 0.5–1 mm long, ***flowers*** 2.5–3.5 mm long, white in anthesis, becoming rose in fruit, white-villous on the hypanthium and along the lower third of the midrib abaxially, the tepals monomorphic, broadly obovate, the stamens exserted, 2.5–4 mm long, the filaments pilose proximally, the anthers pink; ***achenes*** trigonous, brown, 2.5–3 mm long, glabrous.

The hybrid is named for David G. Amme, long associated with the East Bay Regional Park District, now retired, who is known for his work on grasses, especially native grass horticulture, grassland restoration, and roadside management, and as a distinguished author on environmental matters.

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Figure 1. *Eriogonum ×ammei* Reveal & Veilleux

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Figures 2 and 3. *Eriogonum ×ammei* Reveal & Veilleux

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A NEW VARIETY OF *ERIOGONUM LEPTOPHYLLUM* (POLYGONACEAE) FROM EASTERN ARIZONA

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ABSTRACT

Eriogonum leptophyllum var. **vallis-rubrum** Reveal & Clifford, **var. nov.**, is proposed for a low prostrate to spreading subshrub no more than 1.5 dm tall confined to Red Valley, Apache County, Arizona.

One expression of *Eriogonum* not accounted for in the just published *Flora of the Four Corners Region* (Heil et al. 2013) was a low, prostrate to sprawling subshrub that is clearly allied to the much large and distinctly shrubby *E. leptophyllum* (Torr.) Wooton & Standl. (Polygonaceae Juss.; Eriogoneae Dumort.) found throughout much of the Four Corners region of Arizona, Colorado, New Mexico, and Utah.

Eriogonum leptophyllum (Torr.) Wooton & Standl. var. **vallis-rubrum** Reveal & A. Clifford, **var. nov. Type. USA. Arizona.** Apache Co.: Along a dirt road 1.3 mi SW of IR 12, E of Black Lake, at the head of Red Valley, 1.9 air mi SW of White Bridge, New Mexico, and 34.5 air mi NE of Ganado, associated with scattered *Atriplex*, 7240 ft elevation, 36°01'31.2"N, 109°03'49.0"W, T4N, R5W, sec. 31NWSE, 21 Sep 2013, *J.L. Reveal, A. Clifford, & K.D. Heil 9020* (holotype: NY; isotypes: ARIZ, ASU, BH, BRY, CAS, GH, MO, RSA, SJNM, US, UTC). Figures 1–2.

Distinguished from var. *leptophyllum* (Fig. 3) by its prostrate to sprawling subshrubby habit and shorter leaves.

Plants subshrubs, prostrate to spreading, 0.4–1.3 (1.5) dm tall, 0.5–3 dm across; ***leaf blades*** linear to linear-oblanceolate, 0.5–2.5 cm long, 0.1–0.2 cm wide, densely white-tomentose abaxially, essentially glabrous and green adaxially, margins tightly revolute; ***aerial flowering stems*** sprawling to somewhat erect, 2–8 (12) cm long, green, finely papillate above the leaves; ***inflorescences*** compact cymose, 1–5 cm wide, the branches dichotomous, glabrous, papillate, the bracts 3, scalelike, triangular, (0.5) 1–4 mm long; ***peduncles*** absent or erect, 0.05–0.1 cm long, glabrous; ***involucres*** 1 per node, narrowly turbinate, 2–4 mm long, 1–2 mm wide, glabrous, the teeth 5, erect, 0.3–0.7 mm long; ***flowers*** 2.5–4 mm long, the perianth white, glabrous, the hypanthium ¼ length of perianth, essentially monomorphic, oblong to narrowly obovate, the stamens exserted, (2) 3–5 mm long, the filaments sparsely puberulent proximally; ***achenes*** brown, 2.5–3.5 mm long, glabrous..

Flowering Aug-Oct. Clayey flats and slopes, sagebrush communities; 2150–2200 m; Red Valley, Apache Co., Arizona.

Figure 1. Habit of *Eriogonum leptophyllum* var. *vallis-rubrum*.

Figure 2. Detail of the habit of *Eriogonum leptophyllum* var *vallis-rubrum*.

Figure 3. Habit of *Eriogonum leptophyllum* var. *leptophyllum*.

The var. *leptophyllum* is a distinct shrub mostly 4–8 (13) dm tall and 5–15 (18) dm across with leaves generally 2–6 cm long. The variety is found on clayey flats, slopes, and outcrops in mixed grassland and sagebrush communities as well as pinyon-juniper woodlands at elevations that range from 1500–2300 m. It is found in Garfield and San Juan Co., Utah, and adjacent Montezuma Co., Colorado, south into eastern Coconino, Navajo, and Apache cos., Arizona, and in Bernalillo, Cibola, McKinley, Rio Arriba, Sandoval, San Juan, Santa Fe, Taos and Valencia cos. of northwestern New Mexico.

At present the var. *vallis-rubrum* is known only from Red Valley where it is locally common.

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A NEW SPECIES OF *BEGONIA* (BEGONIACEAE) FROM MÉXICO

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ABSTRACT

Begonia motozintlensis Burt-Utley & Utley from Chiapas, México, is described as new, illustrated, and compared to *B. strigillosa* A. Dietr. and *B. cristobalensis* Ziesenh.

Begonia in Chiapas, México is represented by about 48 species, including *B. motozintlensis* that is placed in sect. *Gireoudia* (Kl.) A. DC. because of its rhizomatous habit and staminate and pistillate flowers with two sepals and no petals (Burt-Utley 1984). It is uncommon among species in this section in its elongate rhizomes that freely branch. Like several other rhizomatous Mexican taxa in sect. *Gireoudia*, leaf blades typically have conspicuous maroon maculations, a character which is rare in the Central American taxa (Burt-Utley, pers. obs.).

BEGONIA MOTOZINTLENSIS Burt-Utley & Utley, sp. nov. **TYPE: MÉXICO. Chiapas**. About 7.3 mi N of Motozintla de Mendoza along road to Siltepec and El Porvenir which begins ca 3 mi S of Motozintla, 7400 ft, 28 Dec, 1983, *J. Utley & K. Utley 7373* (holotype: MEXU; isotypes: BM, CAS, DUKE, GH, MICH, MO, NY, US, USF). Figure 1.

Rhizomatous herbs to 45 cm long, branching freely; internodes short to elongate, often slender, (0.3–)1.4–4.3 cm, 1.5–4(–6.5) mm diam, glandular, villous and occasionally with a few lacerate scales intermixed, the trichomes 1–5 mm and a ring of lacerate scales to 3.5–5 mm often at bases of stipules and petioles. **Leaf blades** asymmetric, ovate to elliptic or obovate, 4–10(–12.5) X 2.5–7 cm, basally cordate with the lobes occasionally overlapping, apically attenuate-acuminate, marginally ciliate-dentate to ciliate-denticulate at ends of nerves or sometimes ciliate and undulate or shallowly dentate lobed, above glabrous or with scattered villi above the petiole-blade junction, below minutely glandular and sparingly villous, green or green with conspicuous maroon maculations; 8–10(–11)-palmatinerved; petioles 2.5–19(–23) cm, lanate with fine sericeous villi to (2.5–)3.5–5 mm, becoming sparingly pilose with age, and occasional narrow scales and stout villi, especially subtending the blades; stipules persistent, spreading to reflexed with age, lance-ovate, 6–25 mm X 4–8 mm, marginally entire, revolute, keeled with the keel excurrent apically or subapically, glabrous to villous or the keel only villous to villous-squamose, cystospheres present. **Inflorescences** asymmetric, shorter than to exceeding the foliage, few-many-flowered; peduncles (5–)8–29(–48) cm, glabrous to very sparingly finely pilose with trichomes to 4 mm and minute glandular hairs; lowermost bracts obovate, 10 X 8 mm, marginally densely glandular-ciliate-serrulate. **Staminate flowers** with pedicels 6–12.5(–23) mm, glabrous to occasionally minutely glandular; sepals 2, suborbicular to broadly transversely elliptic, (6–)8–12.5(–15) X (6–)8.5–13 mm, glabrous to minutely glandular, pink; petals wanting; stamens 7–12; filaments 0.4–1.5 mm, free or on a very low torus; anthers obovate to elliptic in outline, 1–2 X 0.7–0.9 mm. **Pistillate flowers** with pedicels (4–)7–13 mm, glabrous to sparingly minutely glandular; bracteoles wanting; sepals 2, elliptic to suborbicular or transversely elliptic, (5.5–)7.5–13 X 8–12.5 mm, glabrous to very sparingly minutely glandular, pink; petals wanting; styles 3, 2–3 mm, fused to ½ their length; stigmas lunate; ovary trilocular with

Figure 1. *Begonia motozintlensis*, isotype (*John & Kathy Utley 7373*, USF).

bipartite placentae, 6–12 mm, glabrous to sparingly minutely glandular. **Capsules** with pedicels (0.7–)0.9–1.5(–2) cm; bodies 0.8–1.5 cm; locule chambers externally appearing oblong, elliptic or ovate, (0.5–)0.7–1.1 X (0.4–)0.5–0.7 cm; wings variable, equal, subequal or unequal, symmetrically to asymmetrically triangular or less commonly asymmetrically ovate, the largest or primary wing 0.7–1.5 X 0.6–1.2 cm, apically acute to acuminate or rounded, the second often equal or subequal to the primary wing, symmetric to asymmetric, triangular to lunate-triangular, (0.4–)0.6–1.1(–1.3) X (0.5–)0.7–1(–1.3) cm, the third triangular, lunate-triangular or lunate, and equal or subequal to the second.

Distribution and habitat. Steep slopes and canyons of montane rain forests and cloud forests between 1900 and 2400 m in southeastern Chiapas, where it can be found growing epilithically on generally shaded steep rocky outcrops or occasionally growing epiphytically. Considering its locations in Chiapas, *B. motozintlensis* is expected to occur in adjacent Guatemala.

Additional specimens examined. **MÉXICO. Chiapas.** Mpio. Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, 1900 m, 17 Nov 1971, *Breedlove & A.R. Smith 22609* (DS); 28 Dec 1972, *Breedlove & Thorne 30977* (DS); SW side of Cerro Mozotal, 11 km NW of jct of rd to Motozintla, along rd to El Porvenir, 2100 m, 21 Nov 1976, *Breedlove 41625* (DS); 23 Nov 1981, *Breedlove & Bartholomew 55721* (DS); 30 Jan 1982, *Breedlove & Almeda 58136* (CAS); 5 km NNW of Buenos Aires on road to Siltepec, 1980 m, 6 Sept 1988, *Breedlove 69786* (CAS). Mpio. Siltepec, ridge above Siltepec on rd to Huixtla, 2000–2400 m, 18 Jan 1973, *Breedlove & A.R. Smith 31895* (DS); Barranca Honda, Siltepec, Oct-Nov 1949, *Matuda 4113* (NY).

Begonia motozintlensis is an attractive rhizomatous species with short to more often long, slender internodes that branch freely and very elongate rhizomes. These are characters that immediately distinguish *B. motozintlensis* from both *B. strigillosa* and *B. cristobalensis*. In *B. motozintlensis* internodes are (0.3–)1.4–4.3 cm X 1.5–4(–6.5) mm, in contrast to those of *B. strigillosa* that are typically unbranched and 0.2–0.8(–1.2) cm X 3–8 mm, while those of *B. cristobalensis* are 1.5–5 X 3–4 mm. Moreover, stipules of *B. motozintlensis* are lance-ovate, 6–25 X 4–8 mm, marginally entire, revolute, keeled with the keel excurrent apically or subapically, glabrous to villous or the keel only villous to villous-squamose, while those of *B. strigillosa* are asymmetric, broadly ovate to triangular, 10–19(–22) X 5–9 mm, entire and glabrous, with a glabrous to vestite keel. In *B. cristobalensis* stipules are typically smaller and asymmetrically ovate to triangular, (4.5–)6–8(–10) X 3–6 mm but are glabrous to villous with a fimbriate keel. Another difference is in the lowermost inflorescence bracts where those of *B. motozintlensis* are marginally densely glandular-ciliate-serrulate, in contrast to those of both *B. strigillosa* and *B. cristobalensis* that are entire. Capsule bodies overlap in size in all three species but differ in their wings. In *B. motozintlensis*, wings are equal, subequal or unequal and the largest or primary wing is symmetrically to asymmetrically triangular or ovate and apically acute to acuminate or rarely rounded, but in *B. strigillosa* wings are always asymmetric and subequal, with the largest asymmetrically triangular to lunate-triangular and apically rounded to acute while in *B. cristobalensis* wings are always unequal and asymmetrically ovate to broadly lunate and rounded to truncate.

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NEW SPECIES OF *BEGONIA* (BEGONIACEAE) FROM GUERRERO, MÉXICO

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ABSTRACT

Three new species of *Begonia* from Guerrero are described, discussed, and illustrated: **B. martinezii** Burt-Utley & Utley, **B. macvaughii** Burt-Utley & Utley, and **B. tlapensis** Burt-Utley & Utley.

Begonia in México is represented by 112 currently recognized species, including the three that are described herein. Of these, 37 of the 56 known taxa with leafy erect stems develop from underground tubers and are characteristic of many species in sect. *Knesebeckia* (Kl.) A. DC., as circumscribed by both Klotzsch (1854) and Alphonse de Candolle (1859, 1864). The Mexican tuberous species, with few exceptions, occur in western and central México and Oaxaca in seasonally dry environments, where their habitats range from areas with tropical deciduous forests to pine-oak or oak forests and rarely cloud forests. In Flora Novo-Galiciana, 19 of the 25 *Begonia* species treated are tuberous (Burt-Utley & McVaugh 2001) and represent just over half the tuberous species from México (Burt-Utley, pers. obs.). Moreover, 17 of the recognized tuberous species are known to develop bulbils in their leaf axils and, in some instances, leafy erect stems grow from the tubers but produce only bulbils, allowing these species to reproduce asexually in the absence of flowering. Once bulbils are dispersed, they can sprout and develop into new, presumably genetically identical tuberous individuals. In Guerrero, there are 21 known tuberous species, including the species described herein, 10 of which produce bulbils in their leaf axils. In contrast to the situation in México, only five tuberous species are reported from all of Central America, and only two of these taxa are endemic there. With the recognition of *B. martinezii*, *B. tlapensis*, and *B. macvaughii*, there are now 28 known *Begonia* species reported from Guerrero.

1. BEGONIA MACVAUGHII Burt-Utley & Utley, **sp. nov. TYPE. MÉXICO. Guerrero.** 12.3 mi N of MEX 200 on MEX 134 from Salitrera to Cd. Altimirano, 1000 ft, 22 Jul 1990, *J. Utley & K. Utley 8531* (holotype: MEXU; isotypes: CAS, DUKE, MICH, MO, NY, UC, US, USF). Figure 1.

Begonia biserrata Lindl. var. *glandulosa* L.B. Sm. & Schub., 1945. Contr. Gray Herb. 154: 23. **TYPE. MÉXICO. Guerrero.** Wet cliffs near Acapulco, 24 Jun 1935, *O.M. Clark 7223* (holotype: NY; isotype: MO!).

Monoecious herbs 3.6–13 dm tall, developing annually from underground tubers 2.2–2.6 cm diam. leafy stems erect, branching freely, occasionally producing solitary large bulbils to 5 mm at the nodes; internodes of main stem elongate, 3–11 cm, sparingly to densely villous with white-clear spreading trichomes 0.5–3 mm, these occasionally appearing glandular tipped. **Leaf blades** decreasing in size from mid-stem to apex, asymmetric, transverse to oblique, rarely almost straight, ovate to narrowly ovate or broadly obovate in outline, 6.5–24 X 2.8–12 cm, basally cordate to very shallowly cordate, apically acute to rounded or acuminate to attenuate-acuminate, marginally usually deeply (2–)3(–5)-lobed, rarely unlobed, the lobe opposite the petiole insertion to ½ the width of the blade or more, lobes acute to rounded or acuminate, ciliate and ciliate-denticulate to ciliate-serrulate,

villous above and beneath; 4–6(–9)-palmatinerved; uppermost blades greatly reduced to wanting, when present frequently very narrowly ovate; petioles decreasing in length from plant base to apex, 2–12 cm, villous with spreading trichomes 1–3 mm; stipules persistent, ascending to spreading, symmetric to asymmetric, the pairs unequal, oblong-ovate to broadly oblong, 2–8 X 1.5–7 mm, marginally ciliate-incised, sparingly villous. **Inflorescences** axillary and terminal, occasionally with a large bulbil at the nodes, few-many-flowered; peduncles 1.3–3.5(–4.5) cm, villous with usually glandular tipped trichomes to 2 mm; bracts persistent to very tardily deciduous, spreading, ovate to oblong or obovate, 2–3.5 X 1.5–2.5 mm, marginally and apically ciliate-laciniate, glabrous to very sparingly villous. **Staminate flowers** with pedicels 0.8–1.7 cm, glandular-villous; sepals 2, ovate or narrowly ovate, (0.9–)1.1–2.1 X 0.6–1.4 cm, apically acute to attenuate-acuminate, marginally sparingly irregularly ciliate to ciliate-denticulate, villous, light to dark pink; petals 2, elliptic to obovate or ovate, (0.7–)1–1.9 cm X (3–)5.5–8 mm, apically rounded to attenuate-acuminate, marginally very sparingly ciliate, glabrous, colored like the sepals; stamens 46–74, monadelphous; filaments 1–1.5 mm; anthers obovoid to ellipsoid, 0.6–1 X 0.6–1 mm. **Pistillate flowers** with pedicels (13–)18–25 mm, glandular-villous; bracteoles wanting; tepals 5 or if 4, then 1 deeply bilobed, subequal, ovate to broadly ovate or obovate, (0.9–)1.2–1.8 cm X (3–)5–12 mm, margins somewhat undulate and occasionally irregularly to regularly ciliate, the outer 3 only villous, light to dark pink; ovaries trilocular with bipartite placentae, (4.5–)8–12 mm, villous to minutely glandular and villous; styles 3, 1–2.5 mm fused to half their length; stigmas bicornute. **Capsules** with pedicels 2.1–4 cm; bodies 1.4–1.9 cm; locule chambers externally appearing obovate to elliptic, (0.8–)1–1.2 cm X 6.5–9.5 mm; wings 3, the primary wing asymmetrically triangular to ovate, (1.3–)1.6–2.1 X 1.2–1.7 cm, marginally sparingly ciliate to ciliate-denticulate distally; the second asymmetrically lunate to symmetrically triangular, 5–13 X 9–14 mm; the third marginiform, and lunate-triangular.

Additional specimens examined. MÉXICO. Guerrero. Mpio. Juan R. Escudero, Los Copalitos cerca El Zapote, 1 Jul 1986, *M.A. Gomez & L. Marquez* (MEXU); Mpio. Mochitlán, Agua de Obispo, 850 m, 12 Jul 1980, *L. Garcia Martinez 86* (MEXU); 890 m, 12 Jul 1981, *J. Pérez Martínez 98* (MEXU); *R. Gonzalez 62* (MEXU); 850 m, 27 Sep 1987, *G. Espinosa Flores 220* (MEXU); Dist. Montes de Oca, Mpio. Montes de Oca, Vallecitos, 11 Jul 1937, *Hinton 10593* (K, LL, UC, US); Mpio. Tierra Colorada, 12 km despues Tierra Colorada, carr. Tierra Colorada-Teconapa, 28 Jun 1985, *G. Espinosa Flores 398* (MEXU); steep limestone banks on Hwy 95 ca 11.4 mi N of Tierra Colorada or 4.5 mi N of Ocotito (km 50), 2800 ft, 17 Jul 1989, *Utley & Utley 8397* (CAS, CGE, GH, IBUG, LL, MEXU, MICH, MO, NY, US, USF); Mpio. Zihuatanejo, 21 km NE de la desviacion a Cd. Altamirano, sobre la carr. Zihuatanejo-Cd. Altamirano, 400 m, 24 Jul 1996, *J. Soto Nuñez, Román de Soto & Soto Román 9654* (MEXU, USF); Mpio. Zihuatanejo, en la Mesita 21 km NE de la desviacion a Cd. Altamirano sobre la carr. Zihuatanejo-Cd. Altimirano, 400 m, 24 Jul 1996, *J. Soto Nuñez, A. Román de Soto & F. Soto Román 9654* (MEXU); 12 mi S of Tierra Colorada, 1200 ft, 20 Jun 1952, *E.H. Cooper & C.M. Rowell 2646* (MICH); 6 mi N of Ocotito, 3000 ft, *H.A. Floyed & C.L. Ryan 317* (MICH); 0.5 mi N of Acahuizotla, 2800 ft, 26 Jun 1954 m *D.F. Herald & E.E. Clark 335* (MICH, TEX); 2 mi S of Acahuizotla, 3000 ft, 16 Jul 1952, *C. Rowell 3090* (MICH); Km 338, 3km beyond Acahuizotla on hwy to Acapulco, 3000 ft, 23 Aug, 1948, *H. Moore & Wood 4722* (BH, MEXU, UC). **Oaxaca.** 20 km N of Pinotepa Nacional, 170 m, *H.M. Hernandez & R. Torres 438* (MEXU).

Etymology. It is a pleasure to name this interesting species in honor of the late Dr. Rogers McVaugh (1909–2009) who collected extensively in western México and undertook Flora Novo-Galiciana. His publications on the travels of 19th century collectors in México have been an invaluable resource for our research with *Begonia* and *Hechtia* (Bromeliaceae).

Distribution and habitat. *Begonia macvaughii* is known only from Guerrero and adjacent Oaxaca between 170 m and 910 m, where it grows along moist roadbanks and stream banks in

Figure 1. *Begonia macvaughii* Isotype (*Utley & Utley 8531*, USF)

evergreen forests, and *bosques tropicales subcaducifolias*, as well as on open, steep, limestone roadbanks. It is expected to occur in Michoacán in the appropriate habitats.

Begonia macvaughii is an attractive species with oblique to transverse, basally cordate leaf blades. It was originally described as *B. biserrata* var. *glandulosa*, but in examining extant specimens and our collections of this latter taxon (*Utley & Utley 8397* and *Utley & Utley 8531*), it became obvious that these specimens represent a distinct species that is readily distinguished from *B. biserrata* by both vegetative and floral characters. Unlike *B. biserrata* with its leaf bases that superficially appear cordate but are cuneate at the petiole-blade junction and bordered on either side by bladeless nerves, those of *B. macvaughii* are unequivocally cordate to very shallowly cordate with the lowermost nerves bordered on either side by blade tissue. Moreover, leaf blades of *B. macvaughii* have distinct leaf apices, in contrast to those of *B. biserrata*, which typically lack them. Interestingly, leaf apices and lobe apices of *B. macvaughii* can vary in form within leaf blades of a single specimen. The persistent stipules of *B. macvaughii* also distinguish this species from *B. biserrata* with its caducous to fugacious stipules. It also appears that *B. macvaughii* is consistently monoecious while *B. biserrata* is very frequently dioecious or sometimes temporally dioecious and rarely monoecious. Inflorescence characters also readily distinguish this species from *B. biserrata*, the most obvious of which is its persistent to tardily deciduous bracts that contrast immediately with the fugacious to caducous bracts characteristic of *B. biserrata*.

2. **BEGONIA TLAPENSIS** Burt-Utley & Utley, **sp. nov.** **TYPE. MÉXICO. Guerrero.** Huamuxtitlán, 1.6 mi S of Huamuxtitlán on Mex 92 or 47.6 mi S of Hwy 190 on rd to Tlapa de Comonfort, ca 3460 ft, 14 Jul 1991, *J. Utley & K. Utley 8639* (holotype: MEXU; isotypes: B, BH, BM, C, CAS, DUKE, F, GH, IBUG, K, M, MICH, MO, NY, UC, US, USF). Figure 2.

Monoecious herbs 8.5–39 cm tall, developing annually from underground tubers to 8 mm diam; leafy stems erect, branching freely; bulbils not evident at nodes; internodes of main stem elongate, (1.8–)3–8.5 cm, lanate to pilose with very fine sericeous trichomes to 6 mm. **Leaf blades** straight, symmetric, broadly transversely oblong-elliptic to deltoid or hemiorbicular, (2–)4–8(–11.5) cm X (2–)6–15 cm, basally cordate, apically shallowly acute or with no distinct apex, marginally shallowly to very shallowly lobed, the lobes acute to acuminate or rounded, and ciliate-doubly dentate to ciliate-doubly serrate, or ciliate-denticulate to ciliate-serrulate, typically densely pubescent to lanate above, lanate below with trichomes matting, or only rarely pilose; 9–11-palmatinerved; petioles typically wanting, rarely to 4 mm; stipules persistent, variable in form, asymmetrically ovate to elliptic, dolabriform or triangular, (5.5–)7–13(–22) X (4–)6.5–13 mm, marginally ciliate to ciliate-denticulate or serrulate, irregularly weakly lobed, pilose above and below, but occasionally glabrous above. **Inflorescences** typically weakly asymmetrically cymose, axillary and terminal, 1–3 times dichotomous, the uppermost inflorescences exceeding the foliage, several-flowered; peduncles (3–)4–9.5 cm, pilose with trichomes 2–4.5 mm; bracts persistent, spreading to ascending, variable in form, orbicular to hemiorbicular, broadly asymmetrically ovate or obovate, the lowermost 4.5–16 X 4–13 mm, marginally ciliate-laciniate to ciliate-serrulate, pilose to lanate. **Staminate flowers** with pedicels 1.1–2.4 cm, glabrous or occasionally sparingly pilose; sepals 2, suborbicular to very broadly ovate or broadly elliptic, 8–13.5 X 8–14 mm, apically acuminate, marginally finely ciliate-denticulate, only rarely sparingly so, externally glabrous to sparingly pilose, white to pale pink; petals 2, obovate, 10–15 X 5.5–10 mm, marginally entire, white to pale pink; stamens 30–61, monadelphous; filaments 0.2–2 mm; anthers broadly obovoid, 0.5–0.8 X 0.5–0.8 mm. **Pistillate flowers** with pedicels (0.9–)1.3–2.5(–3.2) cm, glabrous to sparingly pilose; bracteoles wanting; tepals 5, occasionally persisting on maturing capsules, variable in shape and size, unequal, suborbicular to obovate or broadly obovate, 7.5–10(–14.5) X 4–8(–12) mm, marginally finely ciliate-denticulate, only rarely sparingly so, glabrous to sparingly pilose, white to very pale pink; ovaries trilocular with bipartite placentae, ovuliferous throughout, 7.5–10(–13) mm, glabrous to sparingly pilose; styles 3, 1.5–2 mm, fused to

Figure 2 *Begonia tlapensis*. Isotype (*Utley & Utley 8639*, USF).

half their length; stigmas bicornute, persisting on developing capsules. **Capsules** with pedicels (1.3–)1.9–2.8 cm; bodies 8.5–14(–17) mm; locule chambers externally broadly obovate to transversely elliptic, 6.5–9 X 6–9.5 mm; wings 3, unequal, the largest sometimes weakly arcuate, asymmetrically triangular to ovate-elliptic, 9–16 X 7.5–11 mm; the second and third asymmetrically triangular to ovate and subequal to each other, or occasionally the third shallowly lunate-triangular, 5–10 X 7–10 mm.

Additional specimens examined. MÉXICO. Guerrero. Tlapa, 1300 m, 15 Aug 1972, *E. Matuda 38472* (CAS-[2], MO). **Oaxaca.** Distr. Juxtlahuaca, Laguna Esmeralda de Tecomaxtlahuaca, 12 km SW de San Miguel Tlacotepec, 2690 m, 18 Jun 1982, *R. Cedillo Trigos & R. Torres 1452* (MEXU, USF).

Etymology. *Begonia tlapensis* is named after Tlapa de Comonfort, Guerrero, where Dr. Eizi Matuda first collected this attractive species.

Distribution and habitat. *Begonia tlapensis* is known only from very dry calcareous areas of Guerrero with thorn-scrub vegetation and seasonally dry forests of northern Oaxaca at elevations between 1300 m and 2690 m. The type series is from a very dry region with thorn-scrub vegetation and abundant *Hechtia* and *Opuntia*.

Begonia tlapensis is an attractive species that was abundant at the type locality. Within both the type series and *Matuda 38472*, variation can be observed in pubescence density. Although individuals of this species have predominantly lanate internodes, there are individuals within a population with significantly less dense pubescence, as observed on *Matuda 38472* (MO) that consists of both a lanate specimen and a pilose one. *Begonia tlapensis* can immediately be distinguished from other Mexican *Begonia* by its leaves that consistently lack petioles. Only two other Mexican taxa are known to at least occasionally have apetiolate leaves, *B. monophylla* A. DC., with which *B. tlapensis* appears most closely allied, and *B. angustiloba* A. DC. — both are also from Guerrero and other parts of western México (Burt-Utley & McVaugh 2001).

From *Begonia monophylla*, *B. tlapensis* is distinguished by its well-developed branching stems with several leaves, in contrast to a single large basal leaf and modified stems with much reduced to rudimentary leaf blades. In particularly robust specimens of *B. monophylla*, there may be several slender branches originating from the stem at the lowermost node, each of which will then produce multiple inflorescences (Burt-Utley & McVaugh 2001). *Begonia tlapensis* also differs from *B. monophylla* in its larger stipules [(5.5–)7–13 X (4–)6.5–12.5 mm vs. 5.5–8 X 1.5–4 mm], longer peduncles (3.4–8.3 cm vs. 1.3–5.5 cm), larger staminate sepals (8–13.5 X 8–14 mm vs. 3.5–8 X 2.5–8.5 mm), and larger staminate petals (10–15 X 5.5–10 mm vs. 4–10 X 3–6 mm). *Begonia tlapensis* is readily separated from the usually apetiolate, narrowly lobed leaves of *B. angustiloba* by the lack of bulbils at its nodes, its pilose to lanate pubescence (vs. glabrous), leaf blades with 9–11 primary nerves (vs. 3–4), well-formed upper leaf blades (vs. highly reduced to rudimentary, ovate to linear), and several-flowered inflorescences (vs. 2–3-flowered).

3. BEGONIA MARTINEZII Burt-Utley & Utley, **sp. nov. TYPE. MÉXICO. Guerrero.** MEX 134, 16.8 mi N of Vallecitos de Zaragoza on hwy from La Salitrera to Cd. Altamirano, 6000 ft, 22 Jul 1990, *J. Utley & K. Utley 8538* (holotype: MEXU; isotypes: US, USF). Figure 3.

Monoecious herbs with leafy erect stems to 1 m tall, developing annually from underground tubers 9-11 mm diam, stems branching, often with clusters of small bulbils to 1 mm diam at nodes of stems and inflorescences; internodes of primary stems 5.5–10 cm, glabrous to very sparingly pilose with trichomes to 1 mm; those stems developing from leaf axils very slender. **Leaf blades** oblique,

rarely straight or transverse, ovate in outline, 6.5–13 X 4–7 cm, basally very shallowly to deeply cordate, apically acuminate to attenuate-acuminate, marginally somewhat variable, shallowly 1 or more lobed at ends of major nerves, doubly serrate-crenate, or doubly dentate or serrate and denticulate to serrulate and irregularly ciliate, above appearing glabrous but minutely glandular to very short villous throughout, below glabrous to short villous and minutely glandular, upper blades similar to lower blades but greatly reduced in size; 7–10-palmatinerved; petioles (1.5–)4–9(–12) cm, with a ring of broad villi 1.5–3 mm on the petiole just below the petiole-blade junction, otherwise glabrous to very sparingly villous with trichomes to 0.8 mm; stipules persistent, spreading to reflexed, often asymmetric, broadly to very broadly ovate or deltoid, 2.5–8 X 3.5–8 mm, apically obtuse to truncate, marginally ciliate-denticulate to irregularly ciliate, often minutely glandular and very sparingly villous within, glabrous without. **Inflorescences** axillary and terminal, often producing small clusters of bulbils at bases of branches, symmetrically cymose, appearing 4 or more flowered, usually with 2 male and 2 female flowers; peduncles 5–7.5 cm, glabrous to very sparingly villous; bracts deciduous to persistent, asymmetric, the lowermost broadly ovate to obovate or hemiorbicular, (6–)10–14 X (6–)9–17 mm, unlobed to 2–3 lobed or the 2 bracts fused, marginally irregular ciliate with stalked glandular hairs, denticulate to serrulate, incised or undulate, within sparingly minutely glandular, without minutely glandular and glandular-villous. **Staminate flowers** with pedicels 8–14 mm, glabrous to sparingly glandular or glandular and glandular-villous with trichomes to 1.2 mm; sepals 2, ovate, 18–23 X 14–16 mm, apically acute to acuminate, marginally crenulate to serrulate and glandular with short, stalked hairs, externally irregularly glandular and glandular-villous; petals 2, elliptic to obovate, 14.5–20 X 7–11.5 mm, marginally distally shallowly serrulate-crenulate or undulate, appearing glabrous but minutely glandular; stamens +/- 45–53, monadelphous; filaments 0.5–1.5 mm; anthers obovate to elliptic, 0.9–1 X 0.7–0.8 mm. **Pistillate flowers** with pedicels 5–9 mm, glabrous to conspicuously glandular-villous; bracteoles wanting; tepals 5, variable in shape and size, elliptic to ovate or obovate, 10–18 X 4–9 mm, marginally weakly glandular-crenulate to serrulate, externally glabrous to glandular or glandular and glandular-villous with stalked glandular hairs; ovary apparently trilocular with bipartite placentae, 7 mm, minutely glandular or glandular and glandular-villous with stalked glandular trichomes; styles to 0.7 mm, fused briefly basally; stigmas bicornute. **Capsules** not seen, but ovary wings 3, 2 subequal to each other, triangular and the third appearing marginiform, shallowly triangular to rounded or truncate apically.

Additional specimens examined. **MÉXICO. Guerrero.** Mpio. Atoyac de Alvarez en las Golondrinas, a 22 km NE de Fila de Caballo, 1600 m, 7 Sept 1983, *E. Martínez S.* and *J.L. Villalobos 4239* (MEXU, USF); 15.8 mi by rd N of El Paraiso on rd from Atoyac de Alvarez to Milpillas, 5440 ft., 4 Jul 1982, *Thomas, Rawlins, & Sholes 2883* (NY).

Etymology. *Begonia martinezii* is named after Esteban Martínez at MEXU, who collected this species in 1983.

Distribution and habitat. *Begonia martinezii* is known only from Guerrero, where it has been collected between 1600 m and 1830 m in evergreen forests or on steep, wet, rocky roadbanks of cloud forests. It is likely to occur in adjacent Michoacán in the appropriate environments.

Begonia martinezii is an attractive tuberous species with large staminate and pistillate flowers that rarely has been collected. This species is variable in its indument, as evidenced by the pubescence observed on the type series, *Utley & Utley 8538*, but in other characters the pubescent specimens are identical to those with very sparse pubescence like *Martínez S. & Villalobos 4239* (USF). The presence of clusters of bulbils to 1 mm like the ones observed on *B. martinezii* can be observed on seven other tuberous *Begonia* from western México that are known to produce clusters of small bulbils to 1 mm in their leaf axils.

Figure 3. *Begonia martinezii*. Isotype (*Utley & Utley 8538*, USF).

In certain vegetative characters, *Begonia martinezii* is similar to both the Mexican endemic, *B. boissieri* A. DC. from the states of Guerrero and México and the Guatemalan endemic *B. gracilioides* Burt-Utley & Utley, but it is readily distinguished from these species by both vegetative and floral characters. Bulbils have been observed on stems of *B. martinezii* and *B. gracilioides* but are wanting on specimens of *B. boissieri* examined. Stipules of *B. martinezii*, are persistent and broadly to very broadly ovate or deltoid and similar to those of *B. gracilioides* but differ from the very narrowly triangular to very narrowly oblong or obovate and fugacious stipules in *B. boissieri*. There are differences in the numbers of major nerves among these three taxa. Leaf blades of *B. martinezii* are 7–10-palmatinerved, while those of *B. gracilioides* are 6–8-palmatinerved and those of *B. boissieri* are 10–11(–14)-palmatinerved. A major difference among these species is the form of the uppermost leaf blades. In both *B. martinezii* and *B. boissieri*, the uppermost leaves are somewhat reduced, but have the same shape and conspicuous petioles like their lower leaves. In *B. gracilioides* the uppermost leaves are greatly reduced and almost linear with very short petioles to 3 mm. Uppermost leaves like those observed on *B. gracilioides* also are observed on a number of Mexican taxa including *B. angustiloba* A. DC. and *B. balmisiana* Balmis. It is also significant to note that these leaves are occasionally fused with stipules at the nodes (pers. obs.).

Inflorescences of *Begonia martinezii* and B. *gracilioides* are few-flowered and symmetrically cymose, but those of *B. boissieri* are often many-flowered and weakly to strongly asymmetrically cymose. In both *B. martinezii* and *B. boissieri*, the stems are terminated by elongate peduncles bearing 4 or more flowers, but those of *B. gracilioides* have shorter peduncles and 1–2 flowers. Pistillate flowers also distinguish these three species, with those of both *B. martinezii* and *B. gracilioides* having ebracteolate ovaries, while those of *B. boissieri* have bracteolate ovaries with large bracteoles exceeding the ovaries in length at anthesis and bracteole scars that can be observed at the base of the capsules. There also appears to be a difference in capsule wings, with those of *B. martinezii* having two large, narrow asymmetrically triangular wings subequal to each other and a marginiform wing, in contrast to those of both *B. boissieri* and *B. gracilioides* with unequal wings, with the largest broadly but shallowly asymmetrically ovate or triangular and the other two very shallowly lunate to triangular.

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ELEOCHARIS FALLAX (CYPERACEAE): RECENT COLLECTIONS AND MORPHOLOGICAL COMPARISON WITH *E. AMBIGENS* AND *E. MONTEVIDENSIS*

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ABSTRACT

Recent collections of *Eleocharis fallax* Weatherby expand the species' range to North Carolina and significantly increase knowledge of its habitats. We provide a key, a table of morphological characters, and photos to distinguish it from other similar, outer Coastal Plain species, including *E. ambigens* Fernald and *E. montevidensis* Kunth. All known specimens of these three species from North Carolina are cited.

Since its description from a single site (Weatherby 1922), *Eleocharis fallax* Weatherby has been problematic due to a paucity of specimens for study and uncertainties regarding its specific status. Although his texts are brief, Svenson (1932, 1939), who monographed the genus worldwide, treated *E. fallax* as a distinct species. When Fernald described *E. ambigens* Fernald (1935) he was concerned mostly with distinguishing it from *E. uniglumis* and *E. halophila* and did not mention *E. fallax*. Despite many additional collections of *E. ambigens* since then, botanists have struggled to distinguish it from *E. fallax*, and even Svenson (1947) was led to conclude that *E. ambigens* was merely a form of *E. fallax*. He cited the presence of 3-parted styles and trigonous achenes in some spikes of *E. ambigens*, which normally has 2-parted styles and biconvex achenes. Subsequent authors tended to follow Svenson. For example, Ahles (1968) examined specimens of both entities, yet they treated *E. ambigens* as a synonym of *E. fallax*. Most recently, however, Smith (in Flora North America 2002) treated it as distinct from *E. ambigens* at the species level. Smith provided full descriptions and, along with his key, restored some measure of confidence among botanists that the two entities could be satisfactorily separated.

The scarcity of specimens of *Eleocharis fallax* remains an issue — Smith (2002) cited only Nova Scotia, Massachusetts, and New Jersey as its total range, possibly based on as few as three collections. That three areas with such a long history of botanical exploration should provide only a handful of specimens, representing an entire species, is enigmatic. In the past decade, however, annotation of specimens at NCU and collection of new specimens in North Carolina have expanded the known range of *E. fallax* sensu stricto southward and significantly increased the number of known collections.

Eleocharis montevidensis Kunth shares with these two species long horizontal rhizomes, reddish culm and leaf sheaths, and (on the Atlantic and Gulf Seaboard) maritime or near-maritime habitats. The shape and length of its spikes and the morphology of its scales are similar to those of *E. fallax* and have led to misidentifications. Therefore we have included this widespread species in this discussion.

Methods

Specimens were examined and measured at NCU. A minimum of ten measurements were made of each character, using a standard millimeter rule. Using the key and descriptions in Smith (2002) as a guide, we annotated all NCU specimens originally determined to be *E. ambigens*, *E.*

Table 1. Morphological and habitat characters of *Eleocharis ambigens, E. fallax,* and *E. montevidensis*.

character	ambigens	fallax	montevidensis
horizontal rhizome	pale brown to red-purple, 1.3-2 mm thick, striate, +/- lustrous. [long, 1-2 mm thick]	red-brown to purple-black, 1-2 mm thick, striate, lustrous. [long, 1-2 mm thick]	dark brown to blackish, 1.0-1.5 mm thick, striate, +/- lustrous. [long, 0.7-2 mm thick]
culm height	35-80 cm. [25-80]	40-70 cm. [30-75 cm]	up to 37 cm (Florida), often <25 cm northward. [25-50 cm]
culm width at mid-culm	0.8-1.2 mm.	0.6-0.8 mm.	0.4-0.8 mm.
leaf sheath tooth	callose to short-toothed, up to 0.3 mm. [same]	callose to short-toothed, up to 0.3 mm. [rarely present, not callose]	callose to toothed, up to 0.9 mm. [same]
mature spike shape	elongate, acuminate. [ovoid to lanceoloid]	ovoid to ellipsoid, blunt to acute. [ovoid or subspheric]	short, acute to blunt [ovoid to ellipsoid to subcylindric]
mature spike length	8-19 mm. [5-23]	6-10 mm. [5-12]	5-9 mm. [4-12]
midspike scale apex (do not use lowermost scales)	acute. [acute, rarely obtuse]	broadly rounded, sometimes bluntly acute. [obtuse to acute]	as in fallax. [broadly rounded]
scale transversely wrinkled and/or apex recurved	no. [no]	yes—some to many. [no mention]	apparently all wrinkled; many recurved distally. [yes]
scale color	red-purple fresh, turning brown with age, central stripe and narrow margins hyaline. [medium brown]	reddish brown to brown, central stripe and broad margins hyaline. [red-brown to blackish brown]	quite orangey in living plants, central stripe and broad margins hyaline. [orange-brown]
style	2-fid. [2-fid, sometimes 3-fid]	3-fid. [3-fid or some 2-fid]	3-fid. [3-fid or some 2-fid]
achene color	golden yellow to golden brown. [dark yellow or straminеous]	ditto, varying to gray-brown [dark yellow to medium brown]	gray-brown to blackish [dark brown]
achene ornamentation	pits abundant and narrow. [finely rugulose]	pits far fewer than in ambigens, each pit larger. [finely rugulose]	pits abundant and narrow, but not well defined (ie, very shallow and sometimes obscure). [finely rugulose]
achene shape	unequally biconvex. [biconvex or some compressed-trigonous]	+/- trigonous. [compressed-trigonous or some thickly biconvex]	unequally biconvex to weakly trigonous. [compressed trigonous]
achene body length	1.6-1.8 mm. [not mentioned]	0.9-1.1 mm. [not mentioned]	0.9-1.1 mm. [not mentioned]
tubercle shape	depressed pyramidal, clearly wider than tall. [depressed pyramidal]	pyramidal, not depressed, as high as wide. [same]	+/- evenly triangular. [pyramidal, as high as wide or sometimes depressed]
tubercle height	0.15-0.3 mm. [not mentioned]	0.3-0.5 mm. [not mentioned]	0.25-0.3 mm. [not mentioned]
tubercle color and ornamentation	blackish, with whitish base or collar. [not mentioned]	blackish, with gray-brown base or collar. [not mentioned]	blackish but encrusted with whitish 'scales'. [not mentioned]
habitat	saltmarshes, brackish marshes, marshes close to tidal rivers and estuaries, interdune marshes [coastal fresh to brackish pond shores and marshes]	maritime shrub swamps, maritime wet grasslands, tidal red cedar woodlands. [coastal fresh to brackish ponds, lakeshores, marshes]	dryish margins of maritime wet grasslands, sandy pondshores, dried flatwoods pond, tidal flats, roadside ditches. [fresh ponds, lakes, springs, seeps, marshes, ditches, grasslands]

fallax, and *E. montevidensis*. We created a table of characters through which we discovered additional means of discrimination. Habitats and ranges of the species are augmented with specimens seen at GA and GH.

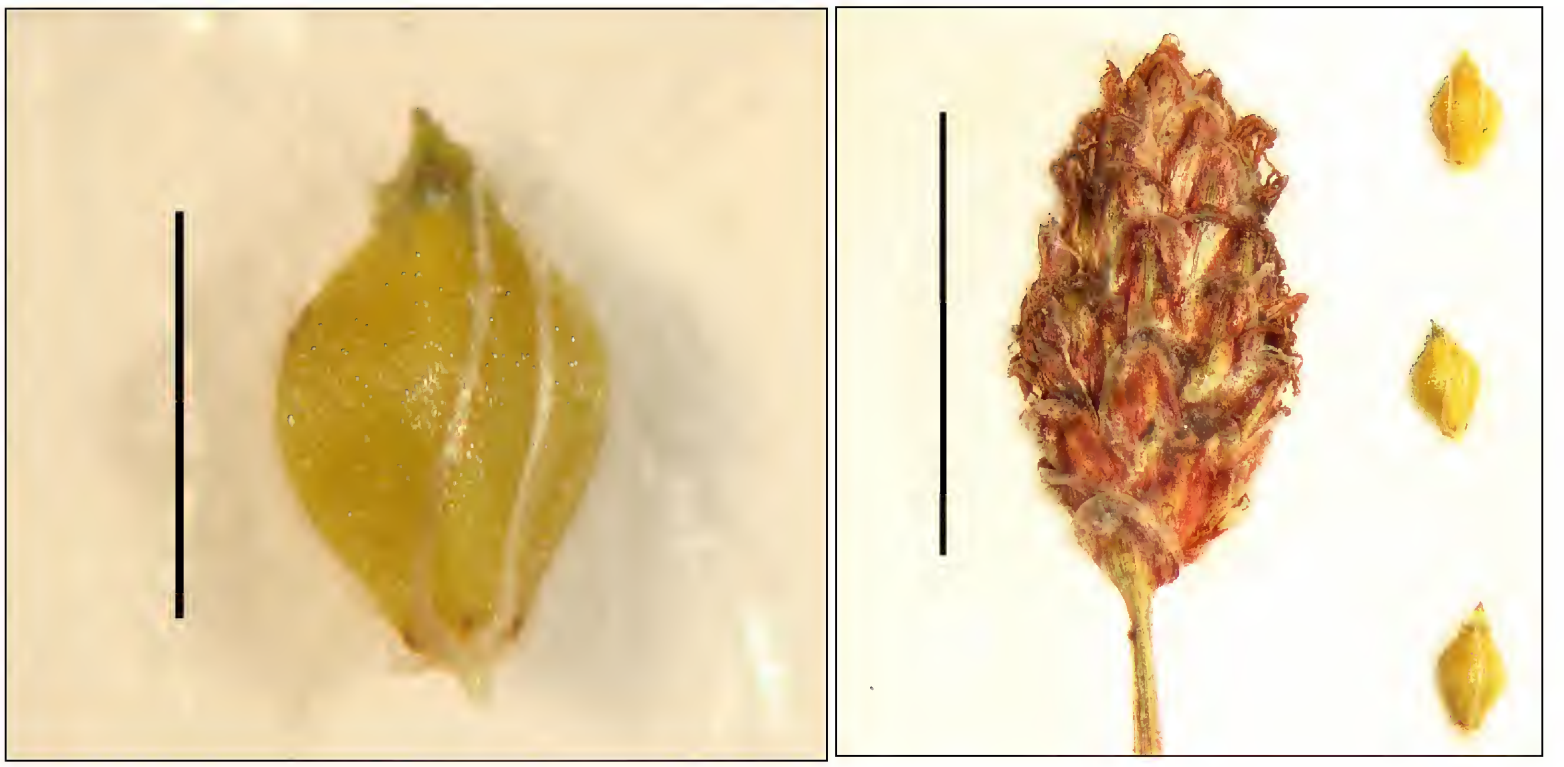

Figure 1. Left, achene of *Eleocharis fallax*. Right, spike and 3 achenes. Scale bar is 1 mm for achene photos; 5 mm for spike photos.

Figure 2. Left, achene of *Eleocharis ambigens*. Right, spike and 3 achenes. Scale bar is 1 mm for achene photos; 5 mm for spike photos.

Figure 3. Left, achene of *Eleocharis montevidensis*. Right, spike and 3 achenes. Scale bar is 1 mm for achene photos; 5 mm for spike photos.

Figure 4. Left, achene of *Eleocharis halophila*. Right, spike and 3 achenes. Scale bar is 1 mm for achene photos; 5 mm for spike photos.

Results and Discussion

Table 1 compares a number of characters useful to distinguish *Eleocharis ambigens*, *E. fallax*, and *E. montevidensis*. Data are from specimens at NCU; data from Smith (2002) are placed within brackets. Note that Smith based his concept of *E. fallax* from specimens collected from only three

localities; in our work we examined specimens from five North Carolina localities not available to Smith (Appendix 1). Discrepancies between Smith's data and ours may in part be due to the greater number of specimens available to us.

Table 1 provides a number of characters, or combinations of characters, which can be used to distinguish *Eleocharis ambigens, E. fallax,* and *E. montevidensis*. We have incorporated the most effective of these in the key below. In the field, two characters are highly useful in separating *E. ambigens* from *E. fallax* and *E. montevidensis*: spike length and culm width. Similarly, short culms and orangey scales indicate that one is viewing *E. montevidensis*. On herbarium sheets, scale color fades and is therefore not reliable on dried specimens, but spike length and culm width retain their utility.

In specimens we examined, achenes of *Eleocharis fallax* are trigonous or rounded-trigonous in cross-section; those of *E. ambigens* are biconvex with one face more tumid than the other. These data contradict statements of Svenson (1947) and of Smith (2002) that occasional achenes of *E. fallax* are biconvex and occasional achenes of *E. ambigens* are trigonous. While Svenson based his decision to synonymize *E. ambigens* within *E. fallax* primarily upon this one achene character, Table 1 suggests that there are other characters that amply separate these two taxa. They include culm width, spike shape and length, achene body and tubercle length, and tubercle shape. Smith (2002) concluded that occasional biconvex achenes and 2-fid styles found in *E. fallax* are insufficient to place *E. ambigens* in synonymy. In our own collections, we have not found biconvex achenes nor 2-fid styles in *E. fallax* sensu stricto. Figures 1-4 depict mature achenes and spikes of these three species plus *E. halophila* (Fernald & Brackett) Fernald, another maritime species that may co-occur with them south to North Carolina.

Key to *Eleocharis fallax* and similar species

This key is derived from Weakley (2012, keys D and E). NOTE: This key is primarily intended to aid those working in the outer Coastal Plain.

1. Achenes lenticular or biconvex, styles 2-branched; perennials or annuals.

2. Tufted or cespitose annuals, rhizomes short or absent ..... **Eleocharis atropurpurea, E. engelmannii, E. geniculata, E. obtusa**

2. Perennial, rhizomes horizontal and elongate.

3. Culms hollow and obviously transversely septate; mostly Coastal Plain Florida and Georgia to Texas and New Mexico; Mexico southward ..... **Eleocharis montana**

3. Culms spongy but not hollow, not septate or septa incomplete.

4. Proximal sterile scales 2–3, the lowest not encircling the base of the spike; northern; in southeastern USA occurs in mountains and piedmont (s to nw Arkansas, n Alabama, w North Carolina) ..... **Eleocharis palustris**

4. Proximal sterile scale 1, encircling the base of the spike; widespread geographically.

5. Achenes prominently pitted (like a honeycomb); tubercles wider than tall (depressed pyramidal), 0.15–0.3 mm tall;brackish and saline habitats of outer Coastal Plain ..... **Eleocharis ambigens**

5. Achenes faintly or obscurely pitted, or smoothish; tubercles taller than wide, 0.35–0.8 mm tall; mountains and piedmont or outer Coastal Plain.

6. Scales obtuse, 30–40 per spike; freshwater habitats mostly of mountains and piedmont, but also of Coastal Plain Delaware, Virginia ..... **Eleocharis erythropoda**
6. Scales acute, 5–30 per spike; brackish and saline habitats of outer Coastal Plain ..... **Eleocharis halophila**

1. Achenes trigonous or nearly so, styles 3-branched; perennial, rhizomes horizontal and elongate.

7. Plants cespitose, often mat-forming, horizontal rhizomes lacking; culm tips often arching and rooting; tubercles confluent with achene and with same texture and color; brackish and saline habitats of outer Coastal Plain, also inland saline microhabitats ..... **Eleocharis rostellata**
7. Perennial, rhizomes horizontal and elongate; culms erect, not rooting; tubercles distinct from achene in texture and color; fresh to brackish habitats of outer Coastal Plain.

8. Culms 40–70 cm tall; scales hyaline with red-brown to blackish brown central stripes; achenes prominently pitted (like a honeycomb); tubercle 0.3–0.5 mm tall ..... **Eleocharis fallax**
8. Culms up to 37 cm tall (reportedly taller, but not verified; in North Carolina-South Carolina, culms mostly are less than 25 cm); scales hyaline with orange-brown to dull orange central stripes (notably orangey in life); achenes faintly or obscurely pitted; tubercle 0.25–0.3 mm tall ..... **Eleocharis montevidensis**

Habitat notes

Eleocharis ambigens inhabits brackish or fresh tidal marshes and ponds. Specifically, these are marshes bordering fresh tidal rivers, marshes within stable interdune swales, and shores of permanent ponds which lie adjacent to ocean beaches or to estuaries. In all cases, salt spray input is frequent and direct intrusion of storm-driven saltwater is occasional. In the case of the specimen from far inland Ouachita Parish, Louisiana, the site may possibly be in saline soils. One current North Carolina population occurs at the edge of a marsh within old forested dunes, along with the halophile/calciphile *Potamogeton illinoensis*.

The type locality for *Eleocharis fallax* is the margin of a fresh tidal inlet on Cape Cod, Massachusetts. Despite numerous attempts, including by the authors, no one has rediscovered this population. We have not examined specimens from Nova Scotia or New Jersey, the only other locations cited by Smith (2002). However, in North Carolina at least five current populations are known. One is in a fresh tidal red cedar forest dominated by *Juniperus virginiana* var. *silicicola*. The others occur in sedge-grass depressional marshes within forested dunes, where they form dense swaths or patches under a broken canopy of *Cornus stricta* and *Salix caroliniana*. Plants are abundant at each locality.

Eleocharis montevidensis is widespread in the New World, extending from the USA to Argentina. In North Carolina it inhabits seasonally wet maritime grasslands and open interdune swales. Within these habitats it occupies drier sandy margins with *Hydrocotyle bonariensis*. Elsewhere on the Atlantic and Gulf Coastal Plain it inhabits roadside ditches, pond and creek margins, and dry tidal flats, all within the range of salt spray.

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Appendix 1. Selected specimens.

ELEOCHARIS AMBIGENS Fernald. **Louisiana**. Orleans Par.: New Orleans, no date, *Cocks s.n.* (GH). Ouachita Par.: 7 mi SSW of West Monroe, frequent in wet clay soil of oak-pine flats, *Kral 8724* (NCU). **Massachusetts**. Dukes Co.: peaty margin of Sheep Pond, Cuttyhunk, 11 Aug 1927, *Fogg 2526* (GH). **Mississippi**. Hancock Co.: Bay St. Louis, salt marsh, 9 May 1970, *Rogers 3240* (NCU). **North Carolina**. Beaufort Co.: freshwater marsh 1 mi SW of Washington, 6 Jul 1958, *Radford 36120* (NCU). Currituck Co.: marsh near causeway to Knott's Island, 27 Aug 1952, *Radford 6560* (NCU). Dare Co.: fresh marsh in Jennette Sedge SE of Doctor's Hill, Buxton, 27 Jun 2013, *Sorrie 13216* (NCU, NCSC). New Hanover Co.: brackish marsh at W end of bridge over Northeast Cape Fear River, Wilmington, 12 Jun 1958, *Bell 13025* (NCU). Pamlico Co.: brackish marsh by Trent Creek, 5 Jul 1958, *Radford 36040* (NCU). Pasquotank Co.: swamp border, branch of Big Flatty Creek, 31 Jul 1958, *Ahles 48134* (NCU). **Rhode Island**. Washington Co.: Block Island, dry sandy shore of Wash Pond, 22 Aug 1913, *Fernald, Hunnewell, & Long 8887* (GH). **Virginia**. James City Co.: James City, small marsh near James River, 8 Aug 1974, *Ware 5711* (NCU). New Kent Co.: shallow water of marsh near York River, 25 Jun 1974, *Soltis 226* (NCU). Princess Anne Co.: marshes bordering ponds, Dam Neck, 30 Jul 1934, *Fernald & Long 3765* (type, GH); swampy border of Rainey Pond outlet, Sand Bridge, 19 Jun 1936, *Smith & Hodgdon* Pl. Exs. Gr. 621 (NCU). Surry Co.: small marsh-bordered pond, Hog Island Waterfowl Refuge, 15 Jun 1974, *Ware 5468* (NCU).

ELEOCHARIS FALLAX Weatherby. **Massachusetts**. Barnstable Co.: fresh to springy border of Dinah's Pond, Yarmouth, 16 Aug 1919, *Fernald & Long 18025* (type NEBC, isotype GH). **North Carolina**. Carteret Co.: marsh in Bogue Barrier woods, 4 mi W of Atlantic City, 24 Jun 1959, *Burk b17-3* (NCU). Dare Co.: Cape Hatteras National Seashore, Mountains-to-Sea Trail, shallow wet swale in *Pinus taeda-Ilex vomitoria* woodland, 11 Jun 2012, *Sorrie 12995* (NCU), Cape Hatteras National Seashore, E of Cape Point Campground, maritime wet grassland, 12 Jun 2012, *Sorrie 13002* (CAHA, NCU), Cape Hatteras National Seashore, marsh near junction of Lighthouse Road and NC 12, 31 May 2013, Sorrie *13187* (GH, NCU). Onslow Co.: New River Marine Corps Air Station, tidal red cedar forest, 29 May 1996, *Leblond & Schafale 4548* (NCU).

ELEOCHARIS MONTEVIDENSIS Kunth. **Alabama**. Mobile Co.: Dauphin Island, moist ditch near water tank, 1 May 1965, *Deramus D452* (NCU). **Florida**. Collier Co.: margin of Palm Creek, W of Everglades, Jul (no year), *Curtiss 3073* (NCU). Franklin Co.: tidal flats along bay at Apalachicola, 9 Jun 1955, *Godfrey 53444* (NCU). St. Johns Co.: moist roadside ditch along Fla. 210, 22 May 1965, *Hodgson s.n.* (NCU). **Georgia**. Chatham Co.: Tybee Island, 1958, *Duncan 20822* (GA). Louisiana. Tangipahoa Par.: wet ditch along route 122, *Allen 8208* (NCU). **Mississippi**. Harrison Co.: vicinity of Biloxi, along beach, 17 Jun 1970, *Rogers 3440* (NCU). Jackson Co.: Moss Point, wet sand, edge of saltmarsh, 3 Jun 1972, *Rogers 8276* (NCU). **North Carolina**. Carteret Co.: near Shackleford Point, 11 Apr 1898, *Ashe s.n.* (NCU). Dare Co.: in wet meadows, Cape Hatteras, 16 Jun 1898, *Ashe s.n.* (NCU), Cape Hatteras National Seashore, maritime wet grassland by Billy Mitchell Airfield, 15 May 2012, *Sorrie 12948* (CAHA, NCU). Hyde Co.: Ocracoke Island, maritime wet grassland, 20 May 2006, *LeBlond 6202* (NCU). Onslow Co.: Camp Lejeune Marine Corps Base, seepage area by Mile Hammock Bay, 30 Aug 1991, *LeBlond 2480* (NCU)

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NEW NAMES IN VERNONIEAE (ASTERACEAE) OF NORTHEASTERN BRAZIL

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ABSTRACT

The monotypic genera *Irwinia* G.M. Barroso, *Oiospermum* Less., and *Pithecoseris* Mart. ex DC. are considered synonyms, respectively, of *Blanchetia* DC., *Centratherum* Cass., and *Chresta* Vell. ex DC., based on morphological analyses. Three new combinations are proposed: **Blanchetia coronata** (G.M. Barroso) Loeuille & Pirani, **comb. nov.**, **Centratherum repens** (Spreng.) Loeuille & Pirani, **comb. nov.**, and **Chresta pacourinoides** (Mart. ex DC.) Siniscalchi & Loeuille, **comb. nov.** Additionally, *Chresta amplexifolia* Dematteis, Roque, & Miranda is synonymized under *Chresta pacourinoides* and the name *Calydermos repens* Spreng. is neotypified.

Monotypic taxa create logical problems by violating the set theoretic basis of Linnaean classification (i.e., Gregg's paradox; Gregg 1954) and indicate unknown relationships (Ebach & Williams 2010). Out of the 131 currently recognized genera in tribe Vernonieae 55 are monotypic; such high proportion of monotypic genera (42%) reflects how poorly understood relationships among members of the tribe are (Keeley et al. 2007; Loeuille 2011). Even though phylogenetic analyses of American Vernonieae in progress (Loeuille 2011 unpubl.; Loeuille et al. in prep.) will help to clarify this situation (e.g. *Pithecoseris* Mart. ex DC.), some rare and poorly known taxa (e.g. *Irwinia* G.M. Barroso and *Oiospermum* Less.) have not been included yet in these analyses. Nonetheless morphological examination of available herbarium specimens of *Irwinia* and *Oiospermum* indicates a close relationship between *Irwinia* and the monotypic *Blanchetia* DC., as well as between *Oiospermum* and *Centratherum* Cass. The required synonymizations are here proposed and detailed.

Synonymization of *Irwinia* under *Blanchetia*

Irwinia coronata G.M. Barroso was described in 1980 based on a single collection from the caatinga of Bahia State, in northeastern Brazil. A close relationship with *Blanchetia heterotricha* DC. was pointed out by the author, since both taxa share an ovoid involucre and two types of trichomes (dark multicellular unbranched trichomes and pale stellate ones with forked arms) which have not been found in other Vernonieae taxa so far (Loeuille 2011). The main reason to establish this taxon as a new genus and not as a new species of *Blanchetia* was, likely, the presence of a biseriate pappus in *Irwinia coronata* (vs. uniseriate in *Blanchetia*). However, the number of pappus series varies frequently between species of a same genus in Vernonieae (e.g., *Eremanthus*, *Lychnophora*, *Paralychnophora*) (Loeuille 2011). Other characteristics cited by Barroso (1980) to set apart *Irwinia* from *Blanchetia*, such as habit (subscandent vs. erect) and number of florets per capitulum (5 vs. 8-10), are commonly used to distinguish species and not genera in Asteraceae. Therefore *Irwinia* is here considered a synonym of *Blanchetia* and the new combination for the only species published in *Irwinia* is provided below.

Blanchetia coronata (G.M. Barroso) Loeuille & Pirani, **comb. nov.** *Irwinia coronata* G.M. Barroso, Rodriguésia 32: 11. 1980. **Type. Brazil. Bahia:** ca. 28 km N de Seabra, estrada para Água de Rega, 1000 m.s.m., 27 Feb 1971, *H.S. Irwin et al. 31174* (holotype: RB!; isotypes: F [scan seen], NY!, US!). Figure 1.

Figure 1. Holotype of *Blanchetia coronata* (*Irwin et al. 31174*, RB)

Additional specimens examined. **BRAZIL. Bahia: Itaberaba**, Chapada Diamantina, 13°43' S, 39°08' W, 30 Apr 2006, *Guedes et al. 12288* (ALCB). **Maracás**, km 16 a 18 da rodovia Maracás-Contendas do Sicorá (BA 250), 27 Apr 1978, *Santos et al. 3212* (CEPEC, HRB). **Wagner**, próximo a Dourados, 12°17' S, 41°07' W, 550 m, 10 Jun 2002, *Bautista & Sarmento 1085* (HRB).

Synonymization of *Oiospermum* under *Centratherum*

The monotypic genus *Oiospermum* Less. shares with *Centratherum* Cass. a herbaceous to subshrubby habit, T-shaped trichomes, a usually solitary capitulum with foliaceous subinvolucral bracts, and a caducous pappus. It is traditionally distinguished from *Centratherum* by the lack of pappus and a unique kind of cypsela setulae. However, a more recently described species of *Centratherum* from Bolivia, *C. cardenasii* H. Rob., also lacks pappus (Robinson 1980a). Robinson (1980a) cited some additional characteristics of *Oiospermum involucratum* (Less.) Nees & Mart. (glabrous phyllaries, style with the pubescent part of the upper shaft very short) aiming to the maintenance of two distinct genera. In absence of a phylogenetic hypothesis including *Oiospermum*, we believe that the classification should explicitly reflect the fact that *O. involucratum* is morphologically closely related to *Centratherum*, rather than maintaining a monotypic genus. Consequently we synonymize here *Oiospermum* under *Centratherum*, and the new combination is provided as follows.

CENTRATHERUM REPENS (Spreng.) Loeuille & Pirani, **comb. nov.** *Calydermos repens* Spreng., Neue Entdeck. Pflazenk. 1: 278. 1821. **TYPE. BRAZIL.** *F. Sello(w) s.n.* (neotype, here designed, P [scan seen] [barcode no. P04339863]). Figure 2.

Ethulia involucrata Nees & Mart. in Wied-Neuwied, Nova Acta Phys. Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 3. 1824. *Ampherephis psilocarpa* Nees & Mart. in Wied-Neuwied, Nova Acta Phys. Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 4. 1824. *Oiospermum involucratum* (Nees & Mart.) Less., Linnaea 4: 339. 1829. **TYPE. BRAZIL.** In Brasiliae arenosis circa San Pedro de Alcantara, 1816, *M.A.P. Prinz zu Wied-Neuwied s.n.* (holotype, P [scan seen] [barcode no. P04388734]). Figure 3.

The species was first described by Sprengel in 1821 as *Calydermos repens*. Sprengel found that his former observation was imperfect ("*manca observatio*") and used the name *Ethulia involucrata* Nees & Mart. in *Systema Vegetabilium* (Sprengel 1826) without giving priority to his epithet for that species. No specimen is cited in either publication. The Compositae of Sprengel's herbarium were sold to Schultz-Bipontinus and are now, through the herbier Cosson, at P in the herbier général (Blake 1930; Stafleu & Cowan 1985). There are two Sellow sheets at P (barcodes P04339863 and P03617811) but only one (P04339863) bears the labels of the Cosson and Schultz-Bipontinus herbaria, therefore this sheet is here chosen as a neotype of *Calydermos repens* Spreng. The holotype of *Ethulia involucrata* has been erroneously attributed to Carl Friedrich Philipp von Martius (1794–1868) by Baker (1873) in *Flora Brasiliensis*; however, the original label was written by Maximilian Alexander Philipp, Prinz zu Wied-Neuwied (1782–1867), who collected in Brazil from 1815 to 1817 (Moraes, pers. comm.).

Additional specimens examined. **BRAZIL. Bahia: Canavieiras**, Vale do Rio Pardo, Oct 1952, *Pinto 52253* (ALCB). **Euclides da Cunha**, 10°30' S, 39°00' W, 20 Mar 2004, *Guedes et al. 10899* (ALCB).

Synonymization of *Pithecoseris* under *Chresta*

Pithecoseris Mart. ex DC. was first described by Candolle (1836), based on a collection by Martius located on the current state of Pernambuco, northeastern Brazil. The description cites lobed leaves with amplexicaul base, fistulose branches, big, congested glomerulus, and dimorphic cypselae. The genus has remained monotypic since then and has been placed in different subtribes throughout its taxonomic history. Currently, it is placed in subtribe Chrestinae, due to the similarity of its pollen type and anther appendages to those in *Chresta* Vell. ex DC. (Robinson

Figure 2 Neotype of *Centratherum repens* (*Sello(w) s.n.*, P).

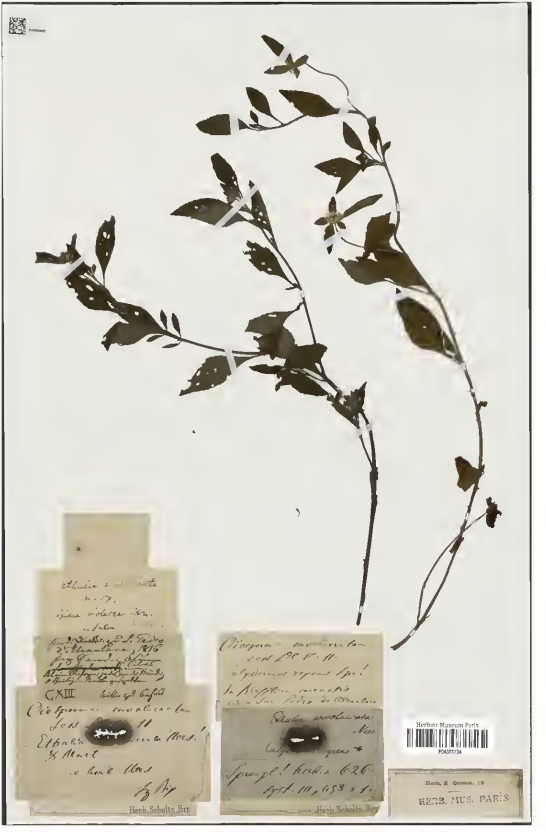

Figure 3. Holotype of *Ethulia involucrata* (*Prinz zu Wied-Neuwied s.n.*, P).

1999). Robinson (1999) also referred to the strangeness of the syncephala in *Pithecoseris*, which are indeterminate, stating that similar forms can be found in *Chresta martii* (DC.) H. Rob.

Under the current circumscription of *Chresta* are included rosulate herbs with syncephaly, and T-shaped trichomes (Loeuille 2011; Loeuille et al. in prep.). *Argyrovernonia* MacLeish has been treated as a synonym of *Chresta* (Robinson 1980b, 1999, 2007), even if its lobed leaves and indeterminate synflorescence differ from those usually found in other members of *Chresta*. Also, species formerly belonging to *Argyrovernonia* are found exclusively in the Brazilian northeast *caatinga*, while regular members of *Chresta* are usually restricted to the *cerrado* and *campo rupestre*. In a recent phylogeny of American Vernonieae, focusing on Brazilian species and using molecular and morphologic data (Loeuille 2011, Loeuille et al. in prep.), *Pithecoseris* emerges as sister-group of *Argyrovernonia*. This implies that if *Argyrovernonia* is maintained as a synonym of *Chresta*, then *Pithecoseris* should also be considered a synonym, in order to keep the whole group monophyletic.

Based on the recommendation of treating a more broadly interpreted *Chresta* (Robinson 1999) in the general morphology of *Pithecoseris*, similar to that of *Argyrovernia* (with lobed leaves and indeterminate syncephala, growing restricted to the *caatingas*), and in order to maintain *Chresta* as a monophyletic taxon, we hereby propose the synonymization of *Pithecoseris* under *Chresta*. The following new combination is provided.

CHRESTA PACOURINOIDES (Mart. ex DC.) Siniscalchi & Loeuille, **comb. nov.** *Pithecoseris pacourinoides* Mart. ex DC. Prodr. 5: 84. 1836. **TYPE. BRAZIL.** Habitat in campis, Provinciae Pernambucanae, *M. von Martius 2529 (550)* (holotype: M [scan seen]). Figure 4, 6.

Chresta amplexifolia Dematteis, Roque & Miranda, **syn. nov.**, Bot. J. Linn. Soc. 157: 587-590. 2008. **TYPE. BRAZIL.** Bahia, Mun. Ipuaçu, Monte Alto, 12°13'55"S, 39°4'35", 12 Aug 2003, *A.C. Pereira et al. 15* (holotype: HUEFS!; isotypes: ALCB!, K [scan seen], CTES). Figure 5.

Chresta amplexifolia Dematteis, Roque, & Miranda has been recently described (Roque et al. 2008) based on a specimen found in Bahia, Brazil, which strongly resembles a smaller form of *Chresta pacourinoides*. Subsequently, on the same inselberg where the type of *C. amplexifolia* was collected, the first author found a large population of *C. pacourinoides* whose individuals present several different morphotypes apparently related to soil depth and degree of sunlight exposure among different spots of the inselberg. Therefore, we conclude that *C. amplexifolia* was based on smaller individuals of *C. pacourinoides* growing on a more exposed environment on the top of the inselberg. Due to general morphology and the environmental implication previously mentioned, we consider *C. amplexifolia* a synonym of *C. pacourinoides*.

Additional specimens examined. **BRAZIL. Bahia: Andaraí,** Chapada Diamantina, 12°48' S, 41°23' W, 2 Sept 1999, *Guedes et al. 6924* (ALCB). **Feira de Santana,** João Durval Carneiro, 12°13 55' S, 39°04.35' W, 12 Aug 2003, *Pereira 15* (HUEFS); 12°13 55' S, 39°04.35' W, 22 Sept 2007, *Loeuille & França 350* (SPF); 12°13.55' S, 39°04.35' W, 22 Sept 2007, *Loeuille & França 351* (SPF); 12°13 55' S, 39°04.35' W, 22 Sept 2007, *Loeuille & França 352* (SPF). **Jacobina,** 25 V.1967, *Costa s.n.* (ALCB); 26 Oct 1978, *Lima et al. 745* (RB); 11°05' S, 40°38' W, 28 Jun 1983, *Coradin et al. 6176* (CEN, RB); Caatinga do Moura, 10 Sept 1960, *Costa s.n.* (ALCB); Serra do Tombador, 30 Oct 1978, *Martinelli et al. 5168* (ALCB, RB); 11°06' S, 40°45' W, 29 Aug 1981, *Ferreira 52* (HRB, HUEFS); 27 Oct 1995, *Carvalho et al. 6154* (CEPEC, NY, US); 11°05.13' S, 40°40.21' W, 2 Jul 1996, *Harley et al. 3330* (ALCB, HUEFS); **Lençóis,** Chapada Diamantina, 18 Aug 1996, *Grillo & Conceição 12* (SPF). **Morro do Chapéu,** Fazenda Jaboticaba, 11°28.18' S, 41°13.56' W, 9 Sept 2006, *Gonçalves & Souza 124* (HUEFS), Cidade das Pedras, 11°40.18' S, 41°01.05' W, 9 Dec 2006, *Guedes et al. 12975* (ALCB). **Palmeiras,** 12°27' S, 41°28' W, 19 Nov 1983, *Noblick & Pinto 2784* (HUEFS); 12 Oct 1987, *Guedes et al. 1565* (ALCB); 12°27.04' S, 41°38.15' W, 12 Oct 1987, *Queiroz et al. 1993* (HUEFS), 12°27.20' S, 41°28.15' W, 25 Oct 1994, *Carvalho et al. 1003* (ALCB, HRB); 12°27.02' S, 41°28.16' W, 29

Figure 4. Holotype of *Chresta pacourinoides* (*Martius 2529 (550)*, M).

Figure 5. Holotype of *Chresta amplexifolia* (*Pereira et al. 15*, HUEFS).

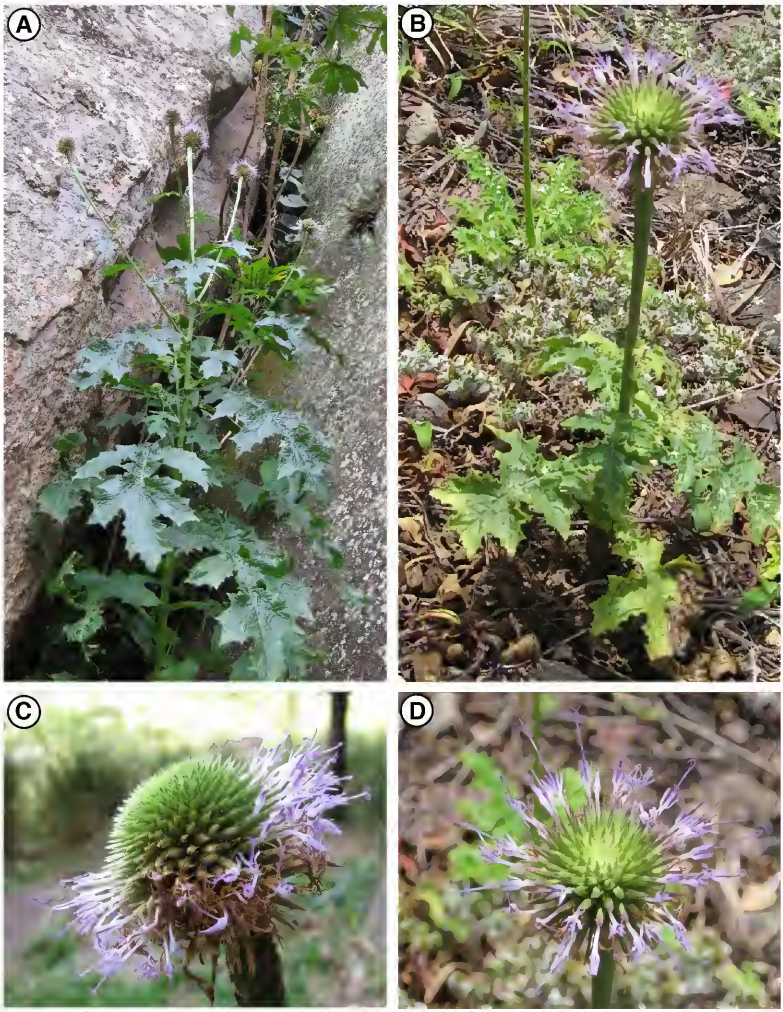

Figure 6. *Chresta pacourinoides*. A, C: habit and syncephala of the morphological type usually associated with *C. pacourinoides*. B, D: habit and syncephala of the morphological type that was described as *C. amplexifolia*. Photos: Benoît Loeuille.

Aug 1994, *Orlandi et al. 504* (ALCB). **Ceará:** *Gardner 1712* (NY, W). **Cedro,** 2 Mar 1933, *Luetzelburg 23748* (RB). **Cratéus,** Ibiapaba, 21 May 1997, *Figueiredo s.n.* (EAC); Serra das Almas, 6 Jun 2001, *Sobrinho & Bruno 109* (EAC); 10 May 2003, *Costa s.n.* (EAC). **Guaramiranga,** 15 Jul 1908, *Ducke 1264* (UB); Serra do Baturité, 2 Jun 1993, *Araujo & Figueiredo s.n.* (EAC). **Ibiapaba,** Serra do Ibiapaba, Jul 1949, *Mello s.n.* (RB). **Independência,** 12 Jun 1979, *Castro & Nunes s.n.* (EAC). **Maranguape,** Serra da Maranguape, 24 Nov 1955, *Lima 2409* (RB); 27 Jun 1981, *Martins & Nunes s.n.* (EAC). **Meruoca,** Serra da Merucoa, 16 Sept 1989, *Fernandes et al. s.n.* (EAC).

Monsenhor Tabosa, Serra da Mata, 19 Jul 1984, *Fernandes & Angélica s.n.* (EAC) **Pacoti,** Pico Alto, 11 Oct 1982, *Angélica s.n.* (EAC); Sítio Olho d´Água dos Tangarás, 24 Jun 1995, *Lima-Verde s.n.* (EAC); Pico Alto, 17 Jun 1989, *Figueiredo s.n.* (EAC). **Quixadá,** Açude Cedro, 31 Aug 1935, *Drouet 2392* (US), 1 Jun 1941, *Bezerra s.n.* (EAC), 12 Jun 1941, *Bezerra 250* (EAC); 4 Sept 2000, *Oliveira 136* (EAC), 23 Jul 1995, *Sérgio & Castro s.n.* (EAC). **Quixeré,** Chapada do Apodi, 5°12' S, 37°48' W, 13 Jun 1996, *Paula-Zárate et al. 244* (EAC); 5°12' S, 37°48' W, 13 Jun 1996, *Paula-Zárate et al. 247* (EAC), 5°11 51' S, 37°46 43' W, 17 Jun 1997, *Barros et al. 146* (EAC). **Santa Quitéria,** Itataia, 7 Jun 1984, *Fernandes et al. s.n.* (EAC), 17 Jul 2005, *Lemos et al. 422* (HUEFS). **Sobral,** Fazenda Macapá, 23 May 1981, *Fernandes & Martins s.n.* (EAC). **Tianguá,** 7 Jul 1997, *Cavalcanti. s.n.* (EAC). **Viçosa do Ceará,** 21 Jun 1972, *Sucre & Silva 9260* (RB); 8 Jun 1991, *Fernandes et al. s.n.* (EAC). **Paraíba: Alagoa Grande,** 24 Sept 1988, *Montenegro, s.n.* (JPB). **Areia,** 20 Sept 1945, *Vasconcellos 2246* (US); Escola de Agronomia do Nordeste, 29 Aug 1953, *Moraes 787* (RB); 8 Aug 1949, *Xavier s.n.* (JPB). **Cabaceiras,** Sítio Bravo, 31 Aug 1992, *Barbosa et al. 1295* (JPB). **Itaporanga,** 25 Mar 1936, *Luetzelburg s.n.* (EAC). **Maturéia,** Pico do Jabre, 7°15 96' S, 37°23 03' W, 11 Jul 2007, *Agra et al. 6976* (JPB). **Pocinhos,** 31 Oct 2007, *Gadelha Neto & Lima 1942* (JPB). **Teixeira,** Pico do Jabre, 7°11 10' S, 37°25.53' W, 18 May 2002, *Agra et al. 5899* (HUEFS). **Pernambuco: Agrestina,** 13 Oct 1966, *Tenório 190* (IPA). **Alagoinha,** 26 Jun 1988, *Pereira 321* (IPA). **Altinho,** Maciço do Tabocas, 8°33 45' S, 36°33 45' W, 1 Nov 1996, *Baracho & Siqueira-Filho 338* (UFP). **Bezerros,** Eng. Riachão, 1 Nov 1959, *Lima 3399* (IPA). **Bonito,** 8 Nov 2003, *Cavalcanti et al. 167* (IPA). **Brejo da Madre de Deus,** Propriedade Bituri, 19 Aug 1980, *Perruci & Maia Filho 1* (RB). **Buíque,** Vale do Catimbau, 23 Jan 2006, *Bocage et al. 1065* (IPA). **Exu,** 6 Aug 1986, *Lima 307* (IPA). **Jaqueira,** Usina Colônia, 8°43.23' S, 35°50.19' W, 15 Nov 2001, *Siqueira-Filho 1191* (UFP). **Pedra,** 23 Jul 1987, *Chappeta s.n.* (IPA). **Pesqueira,** Izabel Dias, 8°01 36' S, 36°35.38' W, 7 Aug 2000, *Cantarelli & Viana 400* (UFP); Serra do Ororubá, 26 Dec 1996, *Siqueira-Filho et al. 457* (UFP). **São Caetano,** Sítio Boqueirãozinho, 8°15.03' S, 36°08.07' W, 16 Oct 2000, *Cantarelli & Viana 472* (IPA, UFP). **Rio Grande do Norte: Felipe Guerra,** Sítio do Boqueirão, 5°36.01' S, 37°41 02' W, 2 Jul 2007, *Oliveira et al. 1924* (MOSS).

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TYPIFICATION OF *HARRISIA FERNOWII* (CACTACEAE)

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ABSTRACT

A paratype of *Harrisia fernowii* is here designated as the lectotype, correcting a previous lectotype designation.

Harrisia fernowi Britton was described from collections in Cuba and living accessions. The two cited paratypes are *Taylor 254* (NY) and a collection by Charles Wright. There are two collection numbers of *Harrisia* from Cuba by Charles Wright but Britton (1908) does not specify either. The protologue of *H. fernowii* states "description mainly from N.Y.B.G. *no. 25766*, collected by Norman Taylor (*no. 254*)" (Britton 1908). The *Taylor 254* specimen consists only of two flower buds in a packet that are mounted along with flowers which were collected from the living plant at the New York Botanical Garden in 1912. The flowers are unavailable as lectotypes since they were collected after publication of the name (Franck 2012). The *Taylor 254* flower buds appear to represent the original collection and are here designated as the lectotype. Franck (2012) mistakenly chose an uncited specimen that likely comprised original material for the lectotype of *H. fernowii* and overlooked the paratypes. McNeill et al. (2012), Art. 9.12 states that "the lectotype must be chosen from among the paratypes" and "if no cited specimens exist, the lectotype must be chosen from among the uncited specimens."

Harrisia fernowii Britton, Bull. Torrey Bot. Club 35: 562. 1908. **LECTOTYPE** (designated here): **CUBA. Santiago de Cuba Prov.**: Oriente, [between] Rio Grande and Rio Ubero, 1906, *Taylor 254* (NY [barcode: 00385813, flower buds only]).

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TAPIRIRA LEPIDOTA (ANACARDIACEAE), A UNIQUE NEW SPECIES FROM THE GOLFO DULCE REGION OF COSTA RICA

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ABSTRACT

Tapirira lepidota Aguilar & Hammel, sp. nov., endemic to Costa Rica, is described as new to science. It differs from all other congeners by its lepidote indumentum (on virtually all parts) of peltate scales. It is compared to the locally sympatric and widespread *T. guianensis* Aubl., a usually much larger tree with smaller fruits that are purple (rather than green) at maturity.

Se describe como nueva para la ciencia *Tapirira lepidota*, endémica a Costa Rica. Difiere de todas las demás especies del género por su indumento lepidoto de escamas peltadas (presentes en todos los órganos). Se compara con la localmente simpátrica y de amplia distribución *T. guianensis*, un árbol comúnmente más grande, con frutos maduros morados y más pequeños.

Tapirira Aubl. (Anacardiaceae) is a smallish genus of forest trees widely distributed in the Neotropics from southern Mexico to Bolivia, Venezuela, Trinidad, the Guayanas, Brazil, and Paraguay. Subsequent to Mori and Mitchell's review (1990), in which five species of *Tapirira* were recognized, two additional species have been described, one from Mexico (Wendt & Mitchell 1995) and most recently another from Ecuador (Barfod 1999). The new species described here as endemic to Costa Rica differs from all others in the genus by its lepidote indumentum of abundant, if easily overlooked, peltate scales. In fact, these scales, though similar to those of the genus *Campnosperma*, once inspired a specialist in the family to reject this species from Anacardiaceae. Nevertheless, we have found no (other) inconsistencies with its inclusion in the family, snugly within the genus *Tapirira*.

Tapirira is distinguished from related genera primarily by its densely indumented pistils and pistillodes, unilocular ovaries, and fruits with a usually cartilaginous to coriaceous, inoperculate endocarp. In Costa Rica, the genus has most often been confused with *Spondias*, which differs most obviously by its leaflets usually with a distinct submarginal vein, usually bisexual flowers with apparently valvate (vs. clearly imbricate) petals, glabrous, (3–)5-locular ovaries, and fruits with a bony endocarp. As pointed out by Mitchell and Daly (1991), in technical details *Tapirira* is most easily confused with *Cyrtocarpa*, comprising five species distributed disjunctly in Mexico and

northern and eastern South America, which differs by its deciduous (vs. evergreen) habit, subsessile (vs. petiolulate) lateral leaflets with eucamptodromous (vs. brochidodromous) venation, glabrous (vs. densely indumented) pistils and pistillodes, 1–5-locular ovaries, and fruits with a bony, operculate endocarp.

TAPIRIRA LEPIDOTA Aguilar & Hammel, **sp. nov. TYPE: COSTA RICA. Puntarenas**: Cantón de Golfito, Puerto Jiménez, Río Piro, camino a Cerro Osa, 8°24' N, 83°17' W, 50 m, 17 Oct 1990 (♀ fl., fr.), *A. Chacón 1109* (holotype: CR (2 sheets); isotype: MO). Figures 1, 2.

Differing from all other species of *Tapirira* by its peltate scales and further differing from the otherwise similar *T. guianensis* by its smaller stature, smaller, included stamens, and slightly larger fruits that are green rather than purple at maturity.

Evergreen, dioecious tree, (5–)10–13(–17) m, with transparent, mucilaginous sap, the trunk with dark brown bark, indistinctly reticulate-fissured or essentially smooth, the branchlets densely lepidote to glabrescent, ± densely aculeate-lenticellate. **Leaves** ± evenly spaced along the branches, the petiole 3–23 cm, moderately or densely lepidote to glabrescent; raquis with indument similar to that of petiole; leaflets (3)4–6 per side; petiolules 0.1–0.8 cm (1–7 cm on terminal leaflet); laminae 7.5–27 × 2.7–8.5 cm, elliptic to (more often) oblong-lanceolate or oblanceolate, basally cuneate to rounded and oblique or (more often) ± symmetrical, apically obtuse to (more often) shortly acuminate, chartaceous to subcoriaceous, the upper surface glabrous, the lower more or less densely lepidote with peltate scales to ca. 0.1 mm; venation brochidodromous. **Inflorescences** axillary to apparently terminal on the distal branches, 10–32.5 cm, ± densely lepidote with peltate scales, the branches also indistinctly and sparsely puberulent with simple trichomes to ca. 0.2 mm. **Flowers** white or cream to yellow, ca. 4 mm in diam., the pedicel 1–2 mm, indistinctly and sparsely puberulent with simple trichomes to ca. 0.2 mm; sepals (calyx teeth) 5, 0.6–1 mm, ± deltate-rounded, ± densely lepidote, the apex sparsely and minutely ciliate; petals 5, 1.4–2 mm, ligulate, sparsely lepidote or (more often) glabrous, the veins straight, sometimes shortly branched. **Staminate flowers** with 10 stamens all ± the same size, the filaments included, to ca. 1 mm, the anthers dorsifixed, to ca. 0.3 mm, broadly ellipsoid; pistillode minute, barely visible as 3–5 ± linear stylodes at the center of the densely lepidote disk, or sometimes the stylodes as large as the styles of pistillate flowers (but lacking ovary). **Pistillate flowers** with the staminodes all ± the same size, to ca. 1 mm, the antipetalous ones perhaps slightly shorter; ovary ± ovoid, to ca. 1.5 mm, densely lepidote; locule 1, with 1 pendent ovule; styles 3 or 4(5), to ca. 0.2 mm, the stigmas ± capitate. **Fruits** green at maturity, 1.4–3 × 1.1–2 cm, ovoid to broadly ellipsoid, densely lepidote to glabrescent, the mesocarp transparent, ± gelatinous, sweet, the endocarp white, 0.4–0.5 mm, cartilaginous, smooth but ± reticulate veined, lacking operculum.

Flowering Feb–Apr, Jul, Sep–Dec; fruiting Jan–Apr, Oct, Dec. Mostly edges of wet forest, on slopes along streams and rivers, sometimes on slopes near the coast, 0–350(–1022) m; Costa Rica (Prov. Puntarenas), southern Pacific slope, in the Fila Costeña and the Golfo Dulce region.

Additional collections examined. **COSTA RICA. Puntarenas**: Cantón de Coto Brus, Dist. Sabalito, orilla del Río Sabalito, 20 Oct 2001 (♂ fl), *J. Gómez-L. 13818* (USJ); 8 Dec 2010 (♂ fl), *R. A. Zahawi & F. Oviedo-Brenes 633* (USJ); Cantón de Osa, Dist. Palmar, Fila Retinto al norte de Palmar Norte, Quebrada Benjamín, 23 Feb 1997 (♀ fl, fr), *B. Hammel & R. Aguilar 20860* (CR, INB); Dist. Sierpe, Bahía Chal, 10 Apr 2001 (fr), *R. Aguilar 6421* (INB); 20 Oct 2001 (♀ fl, fr), *R. Aguilar 6607* (CR, INB); 17 Aug 2001 (fr), *A. Miller et al. 220* (INB, MO); Rincón, cerca del puente sobre el Río Rincón, 15 Mar 2010 (fr), *R. Aguilar 12891* (CR, INB, MO, NY); 4 Nov 2013 (♀ fl), *R. Aguilar 14692* (photo voucher, no specimen made; see <http://www.flickr.com/search/?w=56339362@N03&q=14692>); cerca de Banegas, Los Charcos, 28 Mar 2008 (st), *R. Aguilar 10870* (NY); Drake, Progreso, 8 Dec 2008 (st), *R. Aguilar 11573* (NY); 16 Dec 2008 (st), *R. Aguilar 11578*

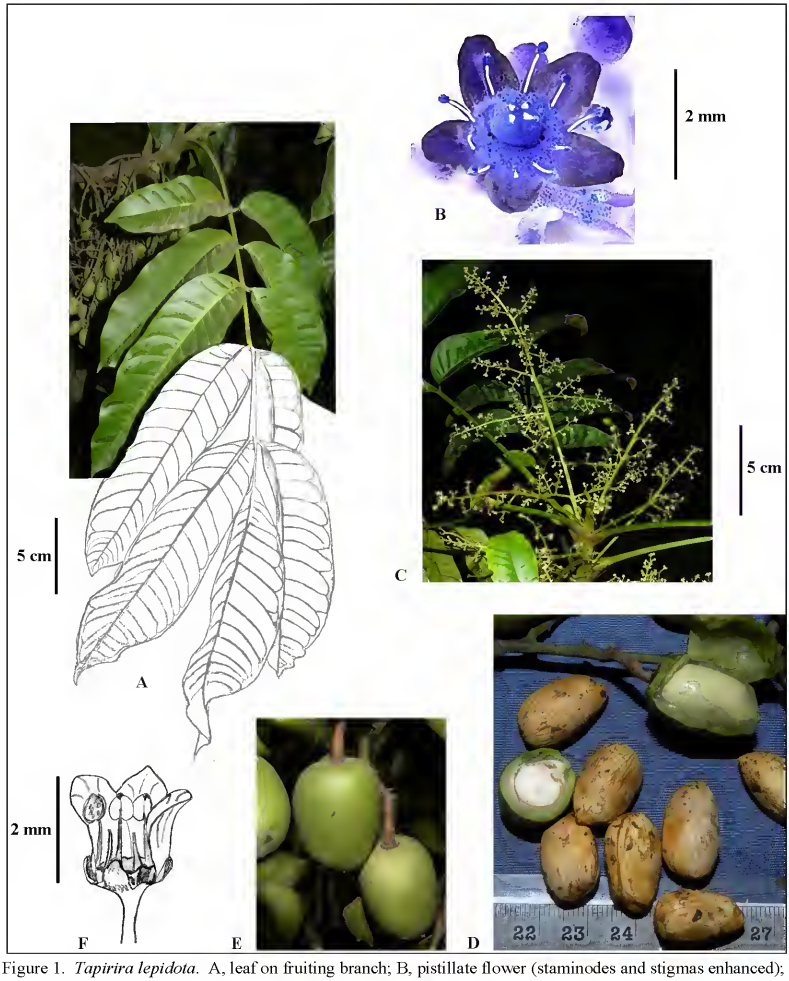

Figure 1. *Tapirira lepidota*. A, leaf on fruiting branch; B, pistillate flower (staminodes and stigmas enhanced); C, inflorescence; D, mature fruit with translucent mesocarp exposed, cleaned endocarps, and fruit cross-sectioned; E, intact mature fruits; F, staminate flower (1 sepal & 2 petals removed, 5 complete stamens and 2 anthers not shown). Photos by R. Aguilar, illustrations by B. Hammel; A, D, and E from *R. Aguilar 12891*; B and C from *R. Aguilar 11561*; F from *Fco. Quesada & M. Segura 795*.

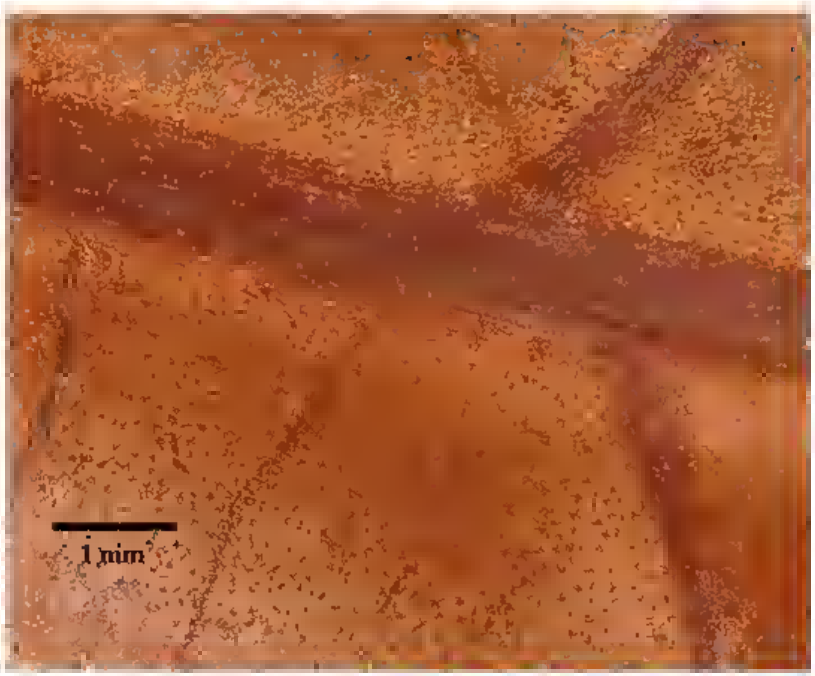

Figure 2 *Tapirira lepidota* Closeup of lower surface of leaflet (midrib at ca mid leaflet) showing peltate scales from *A Chacon 1067*

(NY) Rancho Quemado, camino a Estero Guerra, 11 Mar 2009 (st) *R Aguilar 11922* (NY) Canton de Golfito Dist Jimenez, La Palma, camino a La Tarde, 11 Dec 2008 (♀ fl ft) *R Aguilar 11561* (NY) P N Corcovado Rio Rincon aguas arriba, camino a Cerro Oro 30 Jul 1990 (♂ fl) *G Herrera 4063* (MO) Carbonera, Cerro Osa, 6 Mar 2009 (st) *R Aguilar 11871* (NY) 18 Sep 1990 (♂ fl) *A Chacon 1067* (CR 1NB MO) 3 Km norte de Playa Piro, Puerto Jimenez, Finca Asuncion Esquivel 22 Feb 1989 (fl) *Q Jimenez et al 662* (CR MO) Estacion Agujas, 23 Oct 1997 (♂ fl) *A Azofeifa 481* (INB) Canton de Golfito, P N Corcovado, Valle de Coto Colorado, Punta Estrella y Punta Bejuco, 8 Nov 1993 (♂ fl) *Fco Quesada & M Segura 795* (CR 1NB MO) R N V S Golfito, 28 Feb 1994 (ft) *G Rivera et al 2218* (CR) Mar–Apr 1994 (♂ fl) *G Herrera & G Rivera s n* (USJ) 3 May 2011 (fl) *L D Vargas 4419* (1NB) P N Piedras Blancas, 26 Jan 1999 (ft) *W Huber & A Weissenhofer 1416* (CR)

Tapirira lepidota is a relatively small tree quite common in certain localities, that has been in collections since at least 1989 and has most often been identified as the widespread *T guianensis* (or its synonym *T myriantha* Triana & Planch) also more or less common in Costa Rica and with which it is locally sympatric Other than by its peltate scales, the new species differs from *T guianensis* by its usually smaller stature unbuttressed trunk with relatively smooth bark (vs commonly buttressed with strongly fissured bark) stamens ca 1 3 mm and included (vs to ca 2 mm

and barely included to slightly exserted), and green (vs. purple), slightly larger and ± terete (vs. somewhat flattened) mature fruits with a thinner (0.4–0.5 vs 0.5–1.1 mm; not including the thickened ridge along one side) endocarp. A helpful guide for selecting from among collections of *T. guianensis* for examination under a dissecting microscope as possible additional material of the new species is that the leaflets of the latter dry almost concolorously light to darkish tan, while those of *T. guianensis* most often dry tan abaxially but very dark brown or blackish adaxially. Furthermore, even though the size range of leaflets in the two species overlaps completely, in most specimens the leaflets of *T. lepidota* are larger than those of *T. guianensis*. Although an examination of Panamanian and South American material of *T. guianensis* deposited at MO has not revealed any additional material, the new species might be expected to occur on the Caribbean slope of Costa Rica and Panama (in the Bocas del Toro region) as well as northern South America, areas with which the Golfo Dulce region has shown certain phytogeographical affinities (see e.g., Hammel & Zamora 1993: 411). In any case, the presence of the new species in the vicinity of San Vito at around 1000 m elevation, just a few km from the border with Panama, almost guarantees its occurrence in the latter country.

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TAXONOMY OF *CYCLANTHERA* (CUCURBITACEAE) IN THE USA

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ABSTRACT

All *Cyclanthera* in the USA has traditionally been identified as *C. dissecta* (Torr. & Gray) Arn. but populations there are recognized in the present study to comprise four morphogeographic entities. The type of *C. dissecta*, collected by Thomas Drummond in 1833 or 1834 from the coastal plain of southeastern Texas, represents a rarely collected species endemic to that region. The much more common species of central Texas northward through northeastern New Mexico, eastern Colorado, Oklahoma, Kansas, and south-central Nebraska is identified here as *C. naudtniana* Cogn. Plants in Arizona and New Mexico are identified here as *C. gracillima* Cogn., which continues southward into Mexico and is the species traditionally identified there as *C. dissecta*. *Cyclanthera micrantha* Cogn., endemic to low elevations of Sinaloa and Sonora, Mexico, has sometimes been considered conspecific with *C. gracillima* but is confirmed here as a distinct species. Populations in the trans-Pecos region of Texas are recognized here as **Cyclanthera stenura** Nesom, **sp. nov.** Lectotypes are designated for *C. gracillima*, *C. naudtniana*, and *C. naudiniana* var. *temifolia*.

Cyclanthera Schrader includes about 35 species distributed from the USA south through Mexico and Central America into South America. Plants are monoecious vines characterized by their mostly annual duration, relatively small flowers, androecium of a single, horizontal, continuously circular theca formed from connate anthers, and echinate, few-seeded fruits with explosive dehiscence. *Cremastopus*, comprising two species of northern Mexico, was distinguished by the production of single-seeded fruits, but in all other diagnostic features it is similar to *Cyclanthera*; Kearns and Jones (1992) transferred both species of *Cremastopus* to *Cyclanthera*.

Taxonomy of North American *Cyclanthera* has received considerable recent attention (Jones 1969; Kearns & Jones 1992; Nee 1993; Jones & Kearns 1994; Lira S. 1995, 2001; McVaugh 2001), but a species considered widespread, *C. dissecta* (Torr. & Gray) Arn., has remained heterogeneous in concept — in morphology, ecology, and geography. In the USA, all populations of *Cyclanthera*, from Arizona and New Mexico to trans-Pecos Texas and central Texas northward to Nebraska, have been identified as *C. dissecta*. Another large population system identified as *C. dissecta* is distributed in central and western Mexico, apparently disjunct from the USA plants.

Populations of *Cyclanthera* in the USA occur as four morphogeographic entities (Fig. 1). In the revised view presented here, typical *C. dissecta* is a rarely collected species endemic to the coastal plain of southeastern Texas. Plants of central Texas and south-central USA states previously known as *C. dissecta* are identified here as *C. naudtniana* Cogn. Those from southern Arizona and New Mexico are identified as *C. gracillima* Cogn., which also includes most of the Mexican plants previously identified as *C. dissecta*. Populations from the trans-Pecos region of Texas are recognized here as a previously undescribed species, *C. stenura* Nesom.

Even on a broader geographic scale, plants previously identified as *Cyclanthera dissecta* sensu lato occur mostly as relatively discrete population systems (Fig. 2). With the exception of *C. dissecta* sensu stricto, morphological differences among these systems are relatively slight, which has accounted for their conspecific treatment by recent botanists. As presented here, however, morphological distinctions of the central USA populations (*C. naudtniana*) and those of trans-Pecos

Texas (*C. stenura*), along with their allopatry, support their formal recognition as distinct taxa. The Arizona/New Mexico-northwestern Mexico system, while geographically discrete, has no obvious distinction from that of central Mexico and the two systems are treated here as conspecific (as *C. gracillima*). McVaugh (2001) recognized another Mexican system of *C. dissecta* sensu lato as potentially distinct without formally segregating it (the "upland variant," see comments below) — his observations are only reviewed here and the taxonomy remains to be worked out. With regard to the whole complex, at least it is clear that the name *C. dissecta* can be unambiguously restricted to the populations of southeastern Texas and that plants elsewhere of *C. dissecta* sensu lato should be identified by one or more different names.

Conclusions of the present report are based on study of collections from ARIZ, NMC, UNM, TEX-LL, TAES, SMU-BRIT-VDB, NLU, and MO. Diameters of staminate corollas and anther heads were measured with an ocular micrometer.

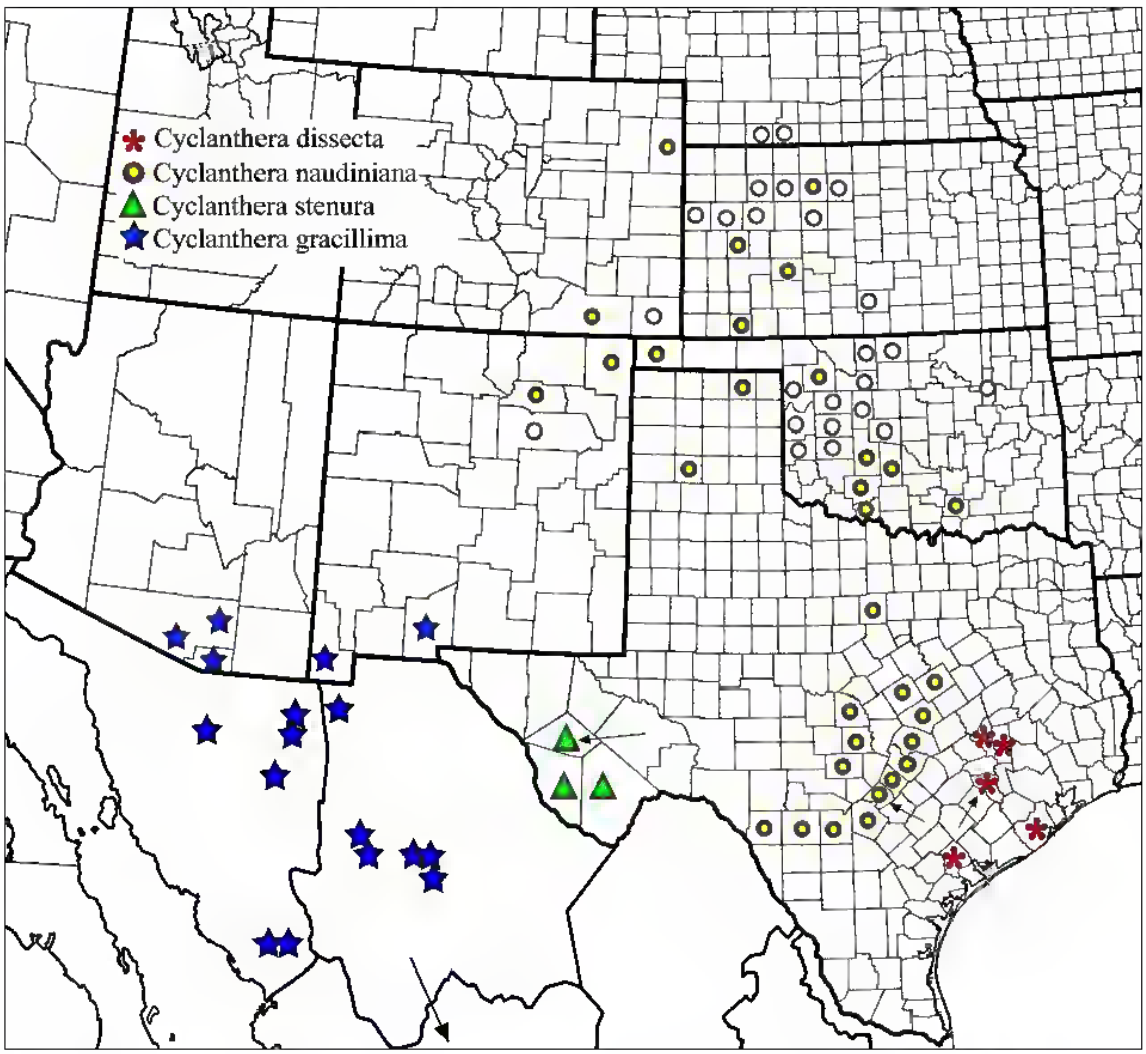

Figure 1. Distribution of *Cyclanthera* species native to the USA. Uncolored symbols are from literature. Arrows point to type localities (the type of *C. gracillima* is from Oaxaca, Mexico).

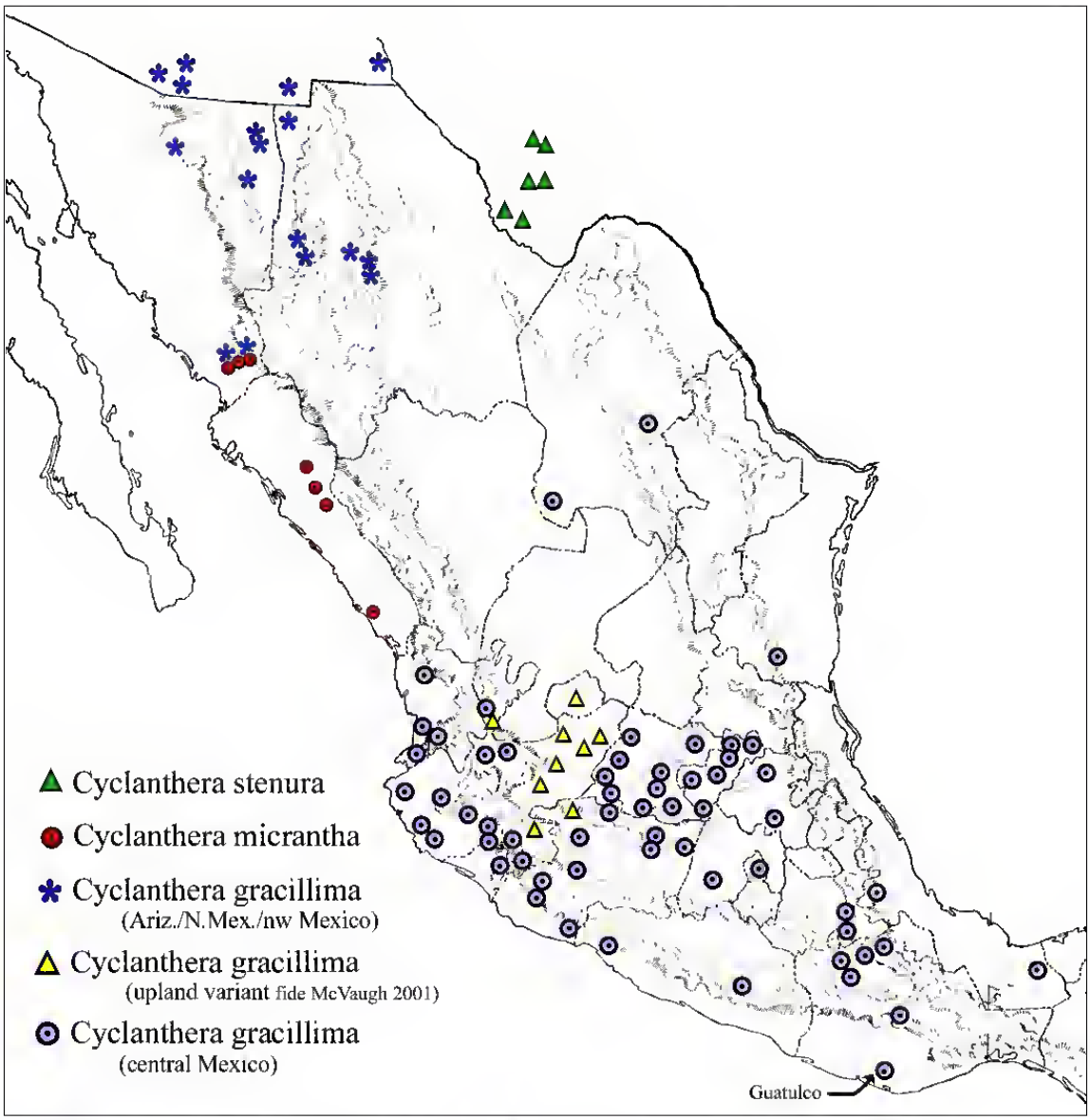

Figure 2. Distribution of *Cyclanthera stenura*, *C. micrantha*, and population systems identified here as *C. gracillima*. Guatulco, Oaxaca, is the type locality of *C. gracillima*. The "upland variant" of *C. gracillima* is mapped from citations by McVaugh (2001). *Cyclanthera gracillima* of "central Mexico" is mapped from a variety of sources: collections examined at TEX-LL and MO, citations by Jones (1969), McVaugh (2001), Lira S. 1995 and 2001, Lira S. & Rodriguez 1999, and Rodriguez 2001.

KEY TO *CYCLANTHERA* SPECIES IN THE USA

1. Staminate inflorescence (1–)7–26-flowered, not laterally branched, floriferous portion 0.2–2.2 cm long.

2. Fruiting peduncles 10–30 mm long, staminate corollas 4.2–6.3 mm in diam., anther head 1.4–2.2(–2.8) mm in diam., usually ciliate ..... **Cyclanthera naudiniana**

2. Fruiting peduncles 2–6 mm long, staminate corollas 2.5–2.8 mm in diam., anther head 0.6–0.8 mm in diam., usually glabrous ..... **Cyclanthera gracillima**

1. Staminate inflorescence (12–)18–90(–130)-flowered, laterally branched, floriferous portion 3–7 or (0.5–)1.2–6 cm long.
   3. Staminate inflorescence (50–)65–90(–130)-flowered, floriferous portion 3–7 cm long lateral branches 3–25 mm long; terminal leaflet consistently lobed ..... **Cyclanthera dissecta**
   3. Staminate inflorescence (12–)18–70-flowered, floriferous portion (0.5–)1.2–6 cm long lateral branches 3–7 mm long; terminal leaflet shallowly to coarsely serrate but not lobed ..... **Cyclanthera stenura**

1. **CYCLANTHERA DISSECTA** (Torr. & Gray) Arn., J. Bot. (Hooker) 3: 280. 1841. *Discanthera dissecta* Torr. & Gray, Fl. N. Amer. 1: 697. 1840. **LECTOTYPE** (McVaugh 2001, p. 531): **USA. Texas**. No locality, 1833 or 1834, *T. Drummond* "Coll. 2. no. 39" (NY digital image!; isolectotypes: BR digital image!-Fig. 3, GH 274888 digital image!).

Thomas Drummond explored the Texas coastal plain in 1833 and 1834, especially along the Brazos, Colorado, and Guadalupe rivers (Geiser 1949). Most of his time was around the town of San Felipe de Austin in Austin County, and the *Cyclanthera* collection probably was made from that area. The type is not specifically mapped here (Fig. 1), but a more recent collection has been made from Austin County.

Two Drummond collections at GH (31859 and 32874), apparently the same species, are noted as "87." Whether these are a separate collection of *Cyclanthera dissecta* or miscopied from "89" is not known.

Stems glabrous except for minutely villosulous ♀ nodes; tendrils 2-branched, branches unequal, rarely (shortest tendrils) unbranched. **Leaves** 3-foliolate, lateral pair of leaflets deeply divided, petiolules 3–5 mm, terminal leaflet 3–4.5 cm, blade broadly lanceolate, petiolule 7–15 mm, linear, abruptly broadening into leaflet base, leaflet margins coarsely serrate to shallowly or deeply lobed; adaxial surface scabrous with hair bases, abaxial surface glabrous; petioles 10–21 mm. **Staminate inflorescence** 5–11 cm, floriferous portion 3–7 cm, (50–)65–90(–130)-flowered, paniculate-racemoid, lateral branches 3–25 mm, longest proximally; flowers pedicellate, solitary, in fascicles of 2–4, or along short axes. **Staminate corollas** 3.5–4.9 mm in diam., white, petals evenly and densely papillate especially distally. **Anther heads** 0.6–0.8 mm in diam, subsessile, glabrous. **Fruiting peduncles** 4–6 mm. **Capsules** 15–25 mm, short-beaked, narrowly ovoid, slightly oblique, spinules 3–4 mm. Figures 3, 4, 5, 6.

Flowering Sep–Nov. Riparian woods and thickets, bottomlands; 20–70 m; Texas. Figure 1.

Additional collections examined. **USA. Texas**. Austin Co.: Stephen F. Austin State Historical Park, on point overlooking Brazos River, forest edge in bottom, 19 Sep 1977, *Lodwick 829* (BRIT). Brazoria Co.: Columbia, common on Bernard, 10 Nov 1899, *Bush 339* (MO); Bay Area scout camp, Camp Karankawa, bank of St. Bernard River, 3.3 mi S of intersect. of FM 1301 and FM 1459, summer 2002, *Rapstein s.n.* (mounted photo filed in BRIT herbarium). Brazos Co.: 3-4 mi N of Navasota on old Hwy 6, [Navasota River bottomland, ca. 200 ft], 16 Oct 1941, *Reeves 1216* and *1216A* (TAES). Grimes Co.: 6.2 mi SW of FR 3090 from its jct with FR 244 to Rock[y] Creek, [ca. 10 air mi N of Navasota; Rocky Creek is tributary to the Navasota River], mesic wooded creekside, with box elder, caric-sedge, elm, oak, 5 Oct 1989, *Jones 3890* (ARIZ, NLU). Victoria Co.: On high E bank of Guadalupe River in Riverside Park, 1.8 air mi NW of jct US Rte 87 and US Rte 59/77 in Victoria, 28º 49.34' N, 97º 1.305' W, locally abundant, climbing over shrubs and high into trees along margin of riparian woodland on deep silty alluvial soils, elev. 60-70 ft, associates include *Carya illinoiensis*, *Celtis laevigata*, *Ehretia anacua*, *Sapindus saponaria* var. *drummondii*, *Melia azedarach*, *Salix nigra*, *Populus deltoides*, *Gleditsia triacanthos*, *Smilax* sp., *Ipomea* sp., *Ampelopsis arborea*, and *Vitis mustangensis*, 24 Sep 2003, *Carr 22218* (TEX).

Figure 3. *Cyclanthera* (Discanthera) *dissecta*, *Drummond 39* (isolectotype, BR). Label data not included on this excerpt of the sheet

Figure 4. *Cyclanthera* (Discanthera) *dissecta* *Drummond 39* (isolectotype, GH).

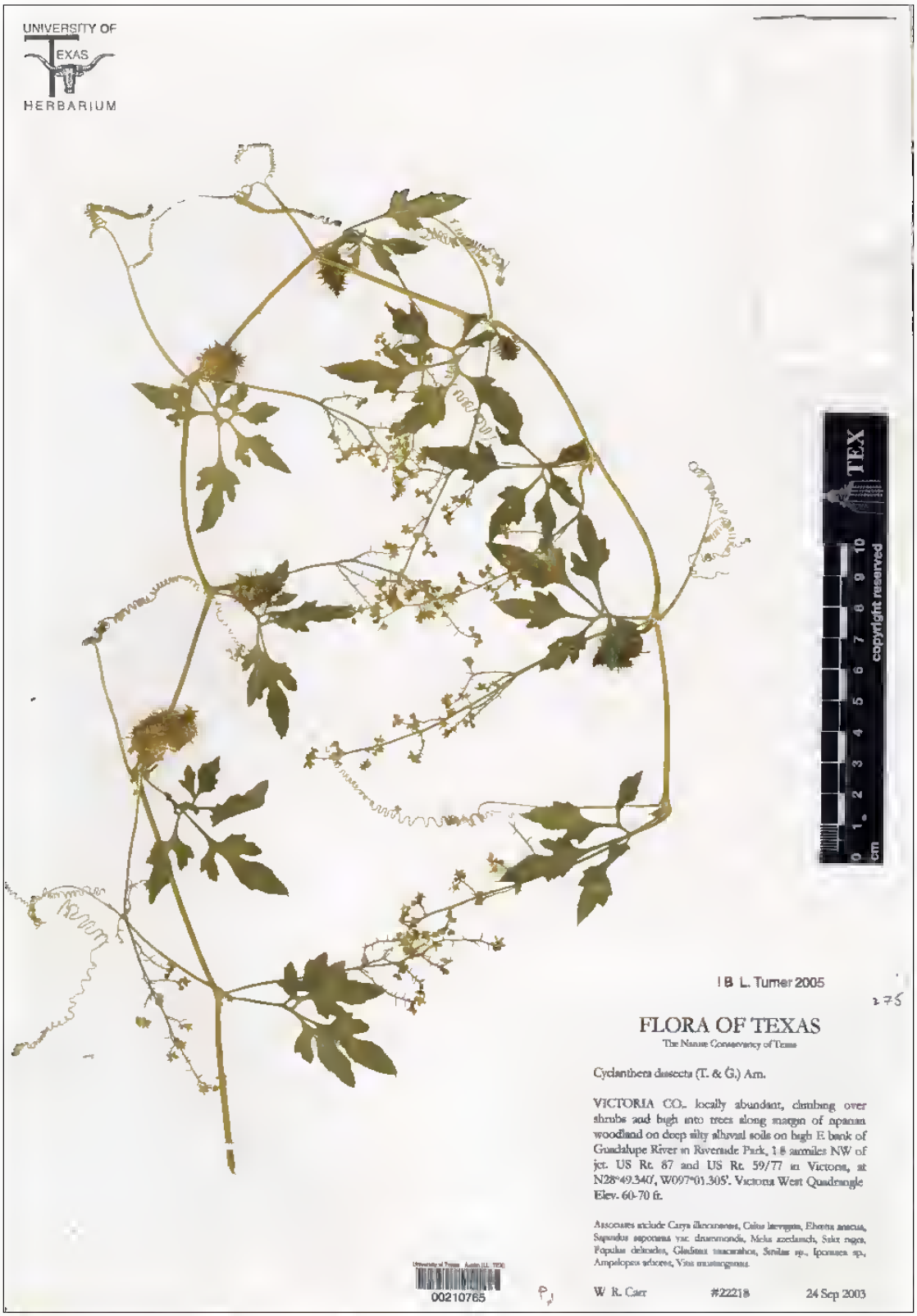

Figure 5. *Cyclanthera dissecta* sensu stricto, coastal plain of southeastern Texas. *Carr 22218* (TEX)

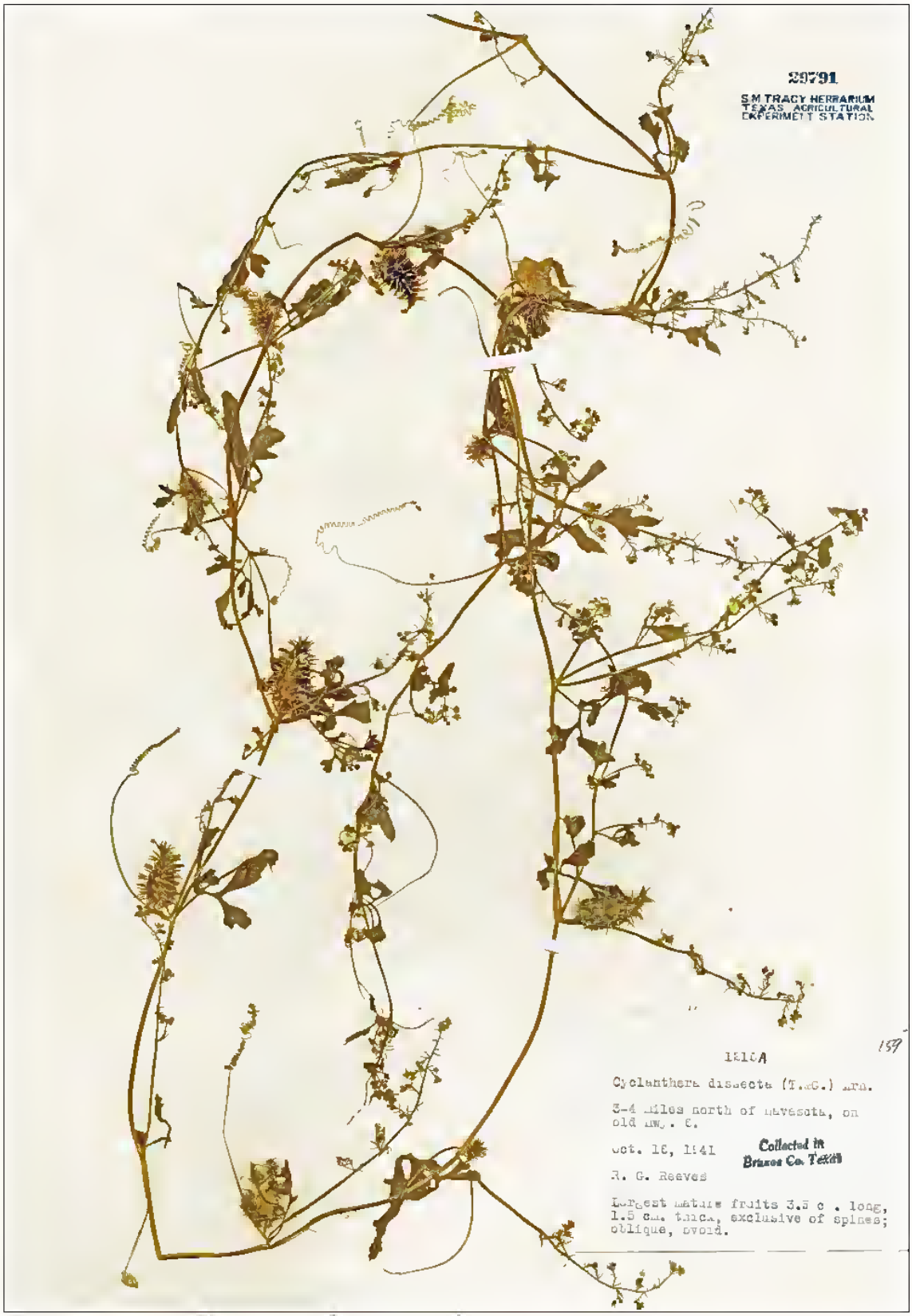

Figure 6. *Cyclanthera dissecta* sensu stricto, coastal plain of southeastern Texas. *Reeves 1216A* (TAES)

Cyclanthera dissecta sensu stricto differs from the plants of central Texas (previously identified as *C. dissecta*, here as *C. naudiniana*) in its smaller staminate flowers and anthers, short fruiting peduncles, and especially in its long-paniculate staminate inflorescences with an abounding number of flowers (Figs. 3, 4, 5, 6). It is remarkable that so few collections have been made (1899, 1941, 1977, 1989, 2002, 2003) since than Drummond encountered it in 1833 or 1834, but this presumably is a reflection of its rarity. The collections in Brazos and Grimes counties were made from localities no more than 6 miles apart, north and northwest of the town of Navasota, suggesting that this area would be a good place to search for more of the species.

The possibility was considered that these Texas coastal plain populations represent a species dispersed northward from Mexico or South America, but I can find no species that is a match. One possibility, *Cyclanthera integrifoliola* Cogn., is relatively widespread in eastern Mexico and southward into Guatemala; the floriferous part of its staminate inflorescence is long (2.5-40 cm), like that of *C. dissecta*, but it rarely produces lateral branches and the flowers are fewer and continuously produced from base to apex of the peduncle, giving it an aspect distinctively different from *C. dissecta*.

Cyclanthera integrifoliola Cogn., Diagn. Cucurb. Nouv. 2: 63, 65. 1877. **LECTOTYPE** (Lira 1995, p. 216) **MEXICO Michoacán** Near Morelia, 6000-7500 ft, 1840, *H.G. Galeotti 7201* (K digital image!; isolectotypes: BR-2 sheets digital images!, G-DEL, P). Lira noted that Galeotti's collection had been chosen as the lectotype by Jones (1969), but the choice by Jones was never validly published.

Cyclanthera integrifoliola var. *angustifolia* Cogn., Diagn. Cucurb. Nouv. 2: 63, 65. 1877. **TYPE: MEXICO [Hidalgo]** Regla, near Rio del Monte, 6000 ft, 1840, *H.G. Galeotti 1901* (holotype: F [as holotype fide Lira & Rodriguez 1999], isotypes: BR digital image!, G-DEL, P). As synonym of *C. integrifoliola* fide Lira (1995).

Cyclanthera integrifoliola var. *major* Cogn., Monogr. Phan. 3: 834. 1881. **TYPE: MEXICO**. Locality not stated, no date, *J.A. Pavon s.n.* (holotype: G [as holotype fide Lira & Rodriguez 1999]. As synonym of *C. integrifoliola* fide Lira (1995).

Cyclanthera donnell-smithii Cogn., Bot. Gaz. 20: 290. 1895. **TYPE: GUATEMALA**. Dept. Quiché. San Miguel Uspantán, 6000 ft, Apr 1892, *E.T. Heyde & E. Lux 3345* (holotype: F [as holotype fide Lira & Rodriguez 1999]; isotypes: GH, K digital image!, NY digital image!, US-2 sheets digital images!). As synonym of *C. integrifoliola* fide Lira (1995).

2. CYCLANTHERA NAUDINIANA Cogn., Monogr. Phan. 3: 831. 1881. **LECTOTYPE** (designated here): **USA. Texas**. [Comal Co.]: Margin of woods and hedges, 1846, *F. Lindheimer 398* (NY-172373; isolectotypes: GH-4 sheets, US digital image!-Fig. 6, MO! digital image!, NY-172371 digital image!, US digital image!). Jones (1969) suggested *Lindheimer 398* as the lectotype but did not choose among the herbaria he cited for the duplicates. Lira S. and Rodriguez (1999) indicated that Jones had selected a NY sheet but did not indicate which one of the two.

Echinocystis pedata Scheele, Linnaea 21: 587. 1848 (not *Cyclanthera pedata* (L.) Schrad., 1831). **TYPE: USA. Texas**. [Comal Co.:] Protologue: "Am Comalcreek bei Neubraunfels auf dem Boden liegend und über niederm Gesträuch rankend" [on the ground and trailing over bushes], Jun, *F. Lindheimer s.n.* (?). *Echinocystis pedata* is perhaps based on the same collection by Lindheimer as *Cyclanthera naudiniana*; Scheele gave only the information quoted here and did not refer to a specific collection number or place of deposition.

Stems glabrous except for minutely villosulous nodes; tendrils unbranched, less commonly 2-branched, branches unequal in length. **Leaves** 3-foliolate, lateral pair of leaflets deeply to nearly completely divided (appearing 5-foliolate), petiolules 1–3(–5) mm, terminal leaflet 3–7 cm, blade lanceolate to narrowly or broadly lanceolate or elliptic-lanceolate, petiolule 5–15 mm, narrowly oblanceolate, gradually broadening into leaflet base, leaflet margins coarsely serrate to shallowly or

Figure 7. *Cyclanthera naudiniana* from central Texas. *Lindheimer 398* (isolectotype, US)

deeply lobed; adaxial surface scabrous with hair bases, abaxial surface glabrous; petioles (5–)15–40 mm. **Staminate inflorescence** 1.2–10.5 cm, floriferous portion 0.3–2 cm, (on shortest axes, 1–)8–27-flowered, racemoid, without lateral branches or lateral branches rarely 2 mm; flowers pedicellate, solitary or in fascicles of 2–3. **Staminate corollas** 4.2–6.3 mm in diam., white, petals minutely and evenly papillate. **Anther heads** 1.4–2.2(–2.8) mm in diam, subsessile, consistently ciliate with a ring of short, white hairs arising just inside the thecal ring. **Fruiting peduncles** 10–30 mm. **Capsules** 15–25 mm, ovoid, barely oblique-gibbous or not at all, short-beaked, spinules 3–5 mm. Figure 7.

Flowering May–Oct. Canyons, rocky slopes, stream sides, riparian woods of elm-hackberry, sycamore, willow-cottonwood, juniper, oak-juniper, pinyon-oak-juniper, live oak, roadsides, open woods; 200–1800 m; Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas. Figure 1.

3. CYCLANTHERA GRACILLIMA Cogn., Diagn. Cucurb. Nouv. 2: 71. 1877. **LECTOTYPE** (designated here): **MEXICO. Oaxaca**. Guatulco, *F.M. Liebman 3325/43* (C digital image!; isolectotype F digital image!). Cogniaux cited *Liebman 43* and *65*; Jones (1969) cited *Liebman 43* as lectotype but did not choose between the C and F duplicates. "Liebm. Pl. Mex. nr. 3325" and "Pl. Mexic. Liebm. Cucurbitacae N. 43" appear to be equivalent.

Cyclanthera naudiniana Cogn. var. *tenuifolia* Cogn., in Monogr. Phan. 3: 831. 1881. **LECTOTYPE** (designated here): **MÉXICO. Veracruz**. Orizaba, 1855, *F. Muller* 589 (K digital image!; isolectotypes: LE, NY digital image!). Lira S. and Rodriguez (1999) indicated that the K specimen was the holotype but Cogniaux cited "In Mexico prope Orizaba (Fr. Müller n. 589 in herb. Kew. et hort. Petrop.)."

Stems glabrous; tendrils unbranched, less commonly 2-branched, branches unequal. **Leaves** 3- or 5-foliolate, lateral pair of leaflets completely or nearly completely divided to base, petiolules 1–4 mm, terminal leaflet 3–5 cm, blade lanceolate to broadly lanceolate or elliptic-lanceolate, petiolule 5–10 mm, linear, abruptly broadening into leaflet base, leaflet margins coarsely serrate to shallowly lobed; adaxial surface scabrous with hair bases, abaxial surface glabrous; petioles 5–10 mm. **Staminate inflorescence** 1.5–10.5 cm, floriferous portion 0.2–2.2 cm, 7–26-flowered, racemoid, without lateral branches; flowers pedicellate, solitary or in fascicles of 2–3. **Staminate corollas** 2.5–2.8 mm in diam., white, petals minutely and evenly papillate. **Anther heads** 0.6–0.8 mm in diam, subsessile, glabrous. **Fruiting peduncles** 2–6 mm. **Capsules** 12–25 mm, short-beaked, narrowly ovoid, slightly oblique, spinules 2–4 mm. Figure 8.

Flowering Aug–Oct. Canyons, arroyos, canyon walls, slopes, stream sides, riparian woods sycamore, cottonwood-sycamore-willow, sycamore-Arizona cypress-oak; 1400–2000 m in the USA, 400–2000 m in northwestern Mexico; Arizona, New Mexico; northwestern Mexico (Chihuahua, Sonora); central Mexico (Nayarit, Jalisco, Michoacan, Colima, Guerrero, Aguascalientes, Guanajuato, Querétaro, Hidalgo, Zacatecas?, Nuevo León?, Coahuila, San Luis Potosí, Tamaulipas, Veracruz, Mexico, Puebla, Oaxaca). Figures 1, 2.

USA collections examined. **Arizona**. Pima Co.: **Baboquivari Mountains**: South Canyon, 15 Sep 1931, *French Gilman B-198* (ARIZ-2 sheets, US); Sycamore Canyon, 22 Oct 1945, *Goodding 237-45* (ARIZ-2 sheets); Moristo Canyon, steep, rocky, N-facing slopes, 23 Oct 1945, *Goodding 250-45* (ARIZ-2 sheets, NY); Toro Canyon, 30 Sep 1934, *Kearney & Peebles 10456* (ARIZ, DS, US); Brown Canyon, above arch, 1460 m, with sycamore, *Muhlenbergia rigens*, *Erythrina*, *Eysenhardtia*, 27 Sep 1997, *McLaughlin 7263* (ARIZ-2 sheets). **Santa Rita Mts.**: Canyon, *Engelmann 92* (MO); *Griffiths & Thornber 143* (US). Cañon of the Santa Rita Mountains, shady damp places, 26 Sep 1880, *Engelmann s.n.* (MO); thickets along creek in Cañon, Santa Rita Mountains, 26 Sep 1880, *Engelmann s.n.* (MO). Santa Cruz Co.: Florida Canyon, 22 Oct 1933, *Harrison & Kearney 9171* (ARIZ, US); Coronado National Forest, basin, left fork, 1 mi S of Florida Station, steep N slope, loam

Figure 8 *Cyclanthera gracillima* from southwestern New Mexico *Wagner 1570* (UNM) Arrow points to staminate inflorescence

soil, with *Bouteloua*, *Hilaria*, *Prosopis*, 4600 ft.,13 Aug 1925, *Magee 258* (RM, fide SEINET). **New Mexico**. [Doña Ana Co.]: Valley of the Rio Grande, below Doñana, *Parry, Bigelow, Wright, & Schott 396* (US). Hidalgo Co.: Animas Mountains, Lower Indian Creek Canyon, streamside, 6000 ft, 13 Sep 1975, *Wagner 1519* and *1570* (NMC). Citations from DS, NY, and US are added from Jones (1969).

Collections examined and mapped from **northwestern MEXICO. Chihuahua**. Mpio. Temosachi, Nabogame, pine/oak/*Cupressus arizonica* forest, 1800 m, 13 Aug 1988, *Laferriere 1604* (NMC, TEX); near Chihuahua, *Pringle 569* (NY, US, fide Jones 1969); mountains near Chihuahua, shaded most bank, 18 Oct 1886, *Pringle 735* (LL, MO; also F, GH, NY, US, fide Jones 1969); ca. 2 air mi S of US border, extreme NW corner of Chihuahua in the N end of the San Luis Mts, W slope of mts. in canyon at end of ranch road, gravelly creek bed, shaded canyon walls, *Cupressus*, *Acer glabrum*, *Quercus hypoleucoides* to 60 ft tall, also with madrone, Apache pine, 9 Oct 1982, *Spellenberg and Soreng 6813* (NMC); Mpio. Madera, Rio Sirupa, 44 km SE de Madera, encinar, 1640 m, 29 Sep 1982, *Tenorio L. 1882* (TEX); Sierra del Nido complex, 20-25 mi NW of Cd. Chihuahua, 1.3 road mi E of Bella Vista, rocky hillside, 6000 ft, 7 Sep 1981, *Worthington 7758* (ARIZ). **Sonora**. Rancho Toma de Agua near San Bernardo, short tree forest, dry canyon bottom, in forest shade, 1500 ft, 13 Sep 1959, *Gentry s.n.* (ARIZ); Sierra de las Gronillas, 2 Oct 1890, *Hartman 98* (GH, US); 15 km E of Navojoa above road to Alamos, summit of Cerro Prieta in the vicinity of the microwave station, thorn forest with *Acacia*, *Bursera*, etc., 400 m, 5 Sep 1989, *Sanders 9259* (ARIZ, TEX); Mpio. Agua Prieta, Rancho El Pinito, Arroyo Cajón Bonito, Sierra San Luis, 56.5 km (by air) ESE of Agua Prieta, Cuenca Los Ojos Foundation conservation area, sycamore-Arizona cypress-oak canyon forest, 1432 m, 23 Sep 2009, *Van Devender 2009-1406* (ARIZ); Mpio. Agua Prieta, Rancho El Diablo, Arroyo Cajón Bonito, ca. 45.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Conservation Area, cottonwood-sycamore-willow riparian forest, 4100 ft, 1 Oct 2009, *Van Devender 2009-1786* (ARIZ); Rio de Bavispe, Cañon de los Apaches, N of Aribabi, *White 2754* (GH, fide Jones 1969).

A New Mexico collection from Sierra County (*Carter & Stevens 3516*, NMC) previously identified as *Cyclanthera dissecta* (as reflected in SEINET) proves instead to be *Echinopepon coulteri* (A. Gray) Rose. I have not been able to examine a similarly identified collection from Grant County (*Huff & Williams 2583*, SNM), but it also may be *Echinopepon* — at least 2583 is out-of-range and out-of-habitat for *Cyclanthera*.

Cyclanthera dissecta in broad sense also has been recognized as a widespread species of Mexico (e.g., Nee 1993; Lira S. 2001; McVaugh 2001; Rodríguez 2001), but these Mexican plants are identified here as *C. gracillima*. Wunderlin (1978) included *C. dissecta* as a disjunct element in the Panama flora, noting that there it "is known only from the Canal Zone, but doubtless occurs elsewhere. It was previously reported from Panama by Cogniaux (1881) as *C. naudiniana*." The plants from Arizona-New Mexico-Chihuahua-Sonora apparently are disjunct from those of central Mexico but apparently indistinguishable in morphology — all are identified here as *C. gracillima* but need for a more detailed study is suggested by the geography.

Gentry's morphological description of *Cyclanthera gracillima* (as *C. dissecta*) for the Sonoran Desert flora (1964) was generalized, as have been others for that region (e.g., Kearney & Peebles 1960; Martin & Hutchins 1981). Descriptions in more recent floristic studies have been more detailed, especially where comparisons of congeneric taxa are involved (e.g., Nee 1993; Lira S. 2001; McVaugh 2001; Rodríguez 2001).

According to McVaugh (2001, p. 534), "In Nueva Galicia there appear to be several regional variants of *Cyclanthera dissecta*, often recognizable but difficult to characterize. It seems that these "variants" differ in habitat preference and in geographical range, as well as in characters of the leaves

and [staminate] inflorescences. I am reluctant to give them names as varieties, because although in the main they are easily recognized, they are based almost wholly on vegetative features, which sometimes vary unpredictably even between leaves or inflorescences on the same plant. There appear to be some differences in flowers and fruits, but the number of observations on these has been so small that no real conclusions can be drawn from them."

McVaugh provided separate descriptions for an "upland variant" and "variants of middle and low elevations" (both variants mapped in Fig. 2). His characterization (p. 535) of one extreme of the middle and low elevation variant apparently is equivalent to what is identified here as *C. gracillima* – – "the central leaflet is often both actually and relatively wider, commonly about twice as long as wide; the ♂ inflorescence tends to be a little longer, mostly 5–10 cm long, the flowers often in a single compact terminal 10–15-flowered cluster."

McVaugh's upland variant was characterized as follows, and in addition to the morphological distinctions it indeed does show a distinct geographical range, essentially allopatric with typical *C. dissecta*. "In moderately arid habitats, 1650–2400 m on the Central Plateau and in adjoining territory. Often marked by a conspicuous many-flowered ♂ inflorescence (6–)9–15 cm long, the flowers often partly in a short terminal raceme, but mostly in sessile lateral fascicles or on lateral branches up to 1.5 cm long, and fruits 20–30 mm long; unfortunately I have not seen the seeds; the central leaflets are relatively narrow, on the average ca 2.8 times as long as wide." The upland variant is similar in its elongate staminate inflorescence to the *Cyclanthera* populations in trans-Pecos Texas described here as *C. stenura*.

Jones (1969) viewed *Cyclanthera dissecta* as "extremely variable in leaf morphology, in the position of the flowers on the peduncle of the male inflorescence, and in the length of the prickles on the fruit" (p. 53). Even so, he proposed to recognize a small group of Pacific Coast plants (Sinaloa and southern Sonora) with relatively long capsular prickles and abbreviated inflorescences at subspecific rank within *C. dissecta*. (as subsp. *micrantha*; McVaugh 2001 treated the same entity, *C. micrantha* Cogn., merely as a synonym of *C. dissecta*). Jones noted that "Taxonomic recognition has been given only to the geographically isolated variant which has extremely long prickles and which occurs only in Mexico in the states of Sinaloa and Sonora" (p. 53). The present study confirms the distinctiveness of these plants, which appear to be appropriately maintained at specific rank (see below for nomenclature and specimens examined; mapped in Fig. 2). The capsular spinules of *C. micrantha* are 6–12 mm long (vs. 2–4 in *C. gracillima*) and their relatively long length is apparent even early in fruit development.

Cyclanthera micrantha Cogn., Contr. U.S. Natl. Herb. 3: 318. 1895. **HOLOTYPE MEXICO. Sinaloa**: Ymala, 25 Sep–8 Oct 1891, *E. Palmer 1706* (US digital image!, isotypes: F-3 sheets digital images!, NY digital image!, UC digital image!). Jones (1969), in his dissertation, proposed to treat *C. micrantha* at subspecific rank within *C. dissecta*, but the nomenclatural combination was never validly published.

Collections examined. **MEXICO. Sinaloa**: Vicinity of Culiacan, 30 Aug 1904, *Brandegee s.n.* (GH, US, as cited by Jones 1969); Palmar, 50-70 mi N of Guamuchil, *Gentry 6103* (MO, also GH and US, as cited by Jones 1969); Culiacan and vicinity, volcanic cerro and valley, thorn forest, heavy clay soil, 150-500 ft, [no date,] *Gentry 7075* (ARIZ), 30 mi by road NW of Mazatlan, hillsides of volcanic rock with deciduous woodland of acacias, columnar cacti, and *Cnidosculus*, ca. 300 ft, 16 Oct 1970, *Webster & Breckson 15642* (ARIZ, TEX). **Sonora**: San Bernardo, Rio Mayo, tropical Sonoran, valley, forest, 24 Aug 1935, *Gentry 1625* (ARIZ, MO, also F and GH, as cited by Jones 1969), stream of the Francas, San Ignacio, *Montes & Salazar 11* (US, as cited by Jones 1969), Mpio. Alamos, Arroyo el Huirotal, E side of the Sierra de Alamos, canyon bottom, riparian tropical deciduous forest, ca. 600 m, 25 Nov 1993, *Steinmann 93-391* (ARIZ), Rio Mayo region, Arroyo de Mentidero at El Chinal road, 11.3 km S of Alamos, arroyo bottom, 240 m, 5 Oct 1992, *Van Devender 92-993* (ARIZ).

4. CYCLANTHERA STENURA Nesom, **sp. nov. TYPE: USA. Texas**. Jeff Davis Co.: ca. 11 mi from Ft. Davis, across road from "Point of Rocks" roadside park on scenic drive, on granite mountain (Woolsack formation), 19 Sep 1966, *D.S. Correll 33710* (holotype: LL!, Fig. 7).

Distinct from *Cyclanthera gracilima* in the more elongate, laterally branched, and profusely flowered floriferous portion of its staminate inflorescence, larger staminate corollas, and narrower and more elongate-attenuate petiolule of the terminal leaflet.

Stems glabrous; tendrils unbranched. **Leaves** 3-foliolate, lateral pair of leaflets deeply lobed, petiolules 2–5 mm, terminal leaflet 3–5 cm, blade narrowly lanceolate, petiolule 3–12 mm, narrowly oblanceolate, gradually broadening into leaflet base, leaflet margins coarsely serrate, adaxial surfaces scabrous with hair bases, abaxial surface glabrous; petioles 16–28 mm. **Staminate inflorescence** (0.5–)2–12 cm, floriferous portion (0.5–)1.2–6 cm, (12–)18–70-flowered, narrowly racemoid, with racemose or fasciculate lateral branches 3–7 mm. **Staminate corollas** 3.8–6.3 mm in diam., white; petals evenly papillate, often indistinctly so. **Anther heads** 0.6–1.0 mm in diam., sessile, glabrous. **Fruiting peduncles** 2–7 mm. **Capsules** (12–)15–20 mm, ovoid, distinctly oblique-gibbous, short-beaked, spinules (2–)3–5 mm. Figure 9. The epithet alludes to the long, narrow, tail-like staminate inflorescence (Greek, *stenos*, narrow, and *oura*, tail).

Flowering (May–)Aug–Oct. Canyons, rocky slopes, among boulders, igneous soil, roadsides, pinyon-oak-juniper; 1150–1800 m; Texas. Figures 1, 2.

Specimens examined. **USA. Texas**. Brewster Co.: Sunny Glen, ca. 5 mi NW of Alpine, 29 Sep 1935, *Sperry T196* (TAES-2 sheets); Sunny Glen, shaded woody slope, 9 Oct 1938, *Sperry T541* (ARIZ, TAES); at Sunny Glen, ca. 6 mi W of Alpine, shaded areas, 29 Sep 1935, *Warnock T31* (TEX); Lover's Rock near Toronto by railroad, ca. 3 mi W of Alpine, 4700 ft, igneous soil, 15 Sep 1964, *Warnock 20496* (TEX). Jeff Davis Co.: SE of Point of Rocks Roadside Park ca. 10 mi W of Ft. Davis, Rte 166, among boulders, small wool sack mountain formation, 10 May 1967, *Correll 34164* (LL); Fern Canyon, 18 Aug 1927, *Cory s.n.* (TAES); Mt. Livermore, Oct 1936, *Hinckley s.n.* (ARIZ); head of Fern Canyon, Mitre Peak Girl Scout Camp, igneous soil, above pool, 4800 ft, 30 Sep 1964, *Keough 245* (TEX); Davis Mountains, rocky slopes, climbing over shrubs and herbs, 5 Oct 1926, *Palmer 31981* (MO, TEX); Lower Madera Canyon ca. 6.5 mi NE of Madera Canyon Roadside Park, Eppenhauer Ranch, slopes above creek, with lichens, mosses, liverworts, *Selaginella*, *Galnum*, and *Heterotheca* in pinyon-oak-juniper woodland, 1 Sep 1984, *Poole 2587* (TEX); Mt. Livermore, 21 Aug 1935, *Hinckley s.n.* (TEX); Davis Mountains, scenic drive S from Kent to HO Canyon, Point of Rocks, 22 Aug 1949, *Tharp & Janszen 49-1132* (TEX); in Fern Canyon, 10 mi N of Alpine, 10 Sep 1941, *Warnock 21438* (TEX); Davis Mountains, Little Aguja Canyon near calf slide, Buffalo Trail Scout ranch, 5300 ft, igneous soil, 8 Aug 1948, *Warnock & Turner 8059* (SMU, TEX); Davis Mts., Point of Rocks Roadside Park along Hwy 166, base of igneous boulders, 5460 ft, 4 Oct 1980, *Worthington 6715* (ARIZ). Presidio Co.: Sierra Tierra Vieja, small canyon just SW of old army post at mouth of ZH Canyon, Espy Miller Ranch, ca. 5000 ft, 7 Sep 1941, *Hinckley 2121* (SMU); Big Canyon above the Fred Shely ranch house; North Chinati Mountains, igneous soil, 3500 ft, 16 Sep 1963, *Warnock 19230* (TEX); Sierra Viaje Mts., Vieja Pass, back of Box Canyon, 4700 ft, growing over shrubs on steep side of canyon, 6 Oct 1979, *Worthington 5411* (TEX).

Additional collections cited by Jones (1969; as *C. dissecta*). **Texas**. Brewster Co.: N of Alpine, Fern Canyon, *Steiger 563* (NY); Alpine, *Steiger 1085* (NY). Jeff Davis Co.: Davis Mts., Mount Livermore, *Hinckley 524* (F, NY); Davis Mts., Mount Livermore, Aug 1936, *Hinckley s.n.* (GH); Limpia Canyon, *Nealley 652* (F); rocky slopes of Davis Mts., *Palmer 31981* (MO); Davis Mts., *Steiger 472* (NY). Presidio Co.: Chinati Mts., *Havard 228* (GH); Sierra Tierra Vieja, Joe Sitter's Canyon, *Hinckley 3377* (GH).

Figure 9. *Cyclanthera stenura* from Jeff Davis County in trans-Pecos Texas *Correll 33710* (LL).

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FURTHER OBSERVATIONS ON THE *OXALIS DILLENII* GROUP (OXALIDACEAE)

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ABSTRACT

Oxalis macrantha (synonym = *O. priceae*) is mostly restricted to limestone substrates (glades, chalk prairies, etc.) in Kentucky, Tennessee, and Alabama and is characterized by its completely hirsute-pilose stems, strongly rhizomatous-colonial habit, and large, red-lined corollas. *Oxalis colorea* also produces hirsute-pilose stems but the distal portions and the pedicels tend to be loosely strigose, and it also differs from *O. macrantha* in its less colonial habit and generally smaller corollas with a variable tendency to produce distinct red lines. Where their ranges meet, *O. colorea* apparently intergrades with *O. florida*, which, in its most distinct form, is a species of the Atlantic coastal plain, although plants in Texas, Louisiana, southwestern Mississippi, Arkansas, and Missouri also are identified here as *O. florida*. *Oxalis texana* produces densely and closely strigose stems like those of *O. dillenii* but differs in its larger, red-lined corollas, less colonial habit, and (in Texas, Louisiana, and Arkansas) characteristically woodland habitat; it is centered in Texas, Louisiana, and Arkansas, but as identified here it also occurs in a disjunct system in southern Alabama and adjacent Florida. County-level distribution maps are provided for *O. texana*, *O. macrantha*, *O. colorea*, and (in part) *O. florida*.

The *Oxalis dillenii* group as recognized here includes *O. dillenii* Jacq., *O. texana* (Small) Fedde, *O. macrantha* (Trel.) Small, *O. colorea* (Small) Fedde, and *O. florida* Salisb., all species native to eastern, southeastern, and south-central USA. *Oxalis dillenii* is the most widely distributed. The most consistent differences among them are primarily in vestiture, corolla size and coloration, and anther/stigma arrangement. Difficulties in identification, at least in some cases, are perhaps more related to infraspecific plasticity in morphology than to hybridization and blurred species bounaries, as sometimes has been assumed. *Oxalis colorea* and *O. florida*, however, apparently intergrade and have been treated as conspecific by Weakley et al. (2012). Further, it is possible that subgroups of plants identified here as *O. texana* and as *O. florida* have had independent origins.

Apparent dysploid variation in chromosome number is known in *Oxalis dillenii* and may be correlated with yet unrecognized variation patterns. Among the other species of the *O. dillenii* group, the chromosome number of only a single population of *O. florida* has been determined. Within sect. *Corniculatae*, the polymorphic *O. corniculata* L. is known to have both dysploid and polyploid

variants and *O. stricta* L. apparently has polyploid variants, at least suggesting that further biological studies in the *O. dillenii* group may be critical toward understanding the variation patterns.

Eiten (1963) reported his study of *Oxalis* sect. *Corniculatae*, which includes the *O. dillenii* group. Lourteig's study of sect. *Corniculatae* (1979) was more detailed in nomenclatural formality but she ignored (obviously intentionally) Eiten's study, not even mentioning or citing it. Nesom (2009) attempted to further clarify the taxonomy of the *O. dillenii* group, differing from Eiten in recognition of some entities and the rank at which they were treated but agreeing in general more closely with Eiten than with Lourteig. The current study again moves closer to agreement with Eiten's earlier concepts of taxa, although nomenclature in some cases is different.

The current study was precipitated by two general observations.

* Field observations in northern Alabama by Spaulding indicated to him that the limestone glade populations identified as *O. macrantha* by Nesom (2009, mistakenly using the later name *O. priceae*) are different from the villous-stemmed plants that generally occur in woodland habitats, thus Nesom's concept of *O. macrantha* included two species.

* Field observations in southern Alabama by Horne and restudy of herbarium material indicated that *Oxalis texana* does indeed occur there. Nesom (2009) restricted its range to Texas, Louisiana, and Arkansas although Eiten (1963) had observed that it occurs eastward to Alabama, Georgia, and Florida. Ward (2004) noted that these putative eastern disjunctions of *O. texana* in Florida were based on misidentifications, but Alabama and Florida collections are tentatively identified here as *O. texana*.

The main observations of the current study are these.

* *Oxalis macrantha* (synonym = *O. priceae*) is restricted mostly to limestone glades in Alabama, Tennessee, and Kentucky. It is distinct from the other hirsute-pilose-stemmed plants sympatric with it in those states, the latter identified here as *O. colorea*. The range of *O. colorea* continues northeastward as far as New Jersey (sporadically from North Carolina northward).

* *Oxalis florida* is a species primarily of the Atlantic coastal plain, although plants in Texas, Louisiana, southwestern Mississippi, Arkansas, and Missouri are identified here as *O. florida*. Intermediates between *O. florida* and *O. colorea* apparently occur where their ranges meet.

* *Oxalis texana* is centered primarily in Texas, Louisiana, and Arkansas. Plants tentatively identified here as *O. texana* in southern Alabama adjacent Florida are slightly atypical and may prove to be more closely related to *O. colorea*, *O. florida*, or *O. dillenii*.

Key to species of the *Oxalis dillenii* group

1 Stems strigose, hairs straight, closely appressed, and usually dense (rare central Louisiana populational variants of *O. texana* irregularly villous proximally), petals with or without red lines at base

2 Flowers 1 or 2–3(–5, very rarely to 8) in umbelliform (rarely irregular) cymes, mostly homostylous; petals 6–12 mm, all yellow, not red-lined at base, plants single-stemmed or caespitose to colonial from rhizomes or rhizomelike branches, open areas, often disturbed ..... **Oxalis dillenii**

2. Flowers (2–)3–5(–8) in umbelliform cymes, very rarely irregular cymes, distylous, petals 11–15 mm (Arkansas, Louisiana, Texas) or 6–12 mm (Alabama, Florida), red-lined at base, plants caespitose or with short stolon-like offsets, sandy woodlands (Texas, Louisiana, Arkansas) or open, disturbed sites (Alabama, Florida) ..... **Oxalis texana**

1 Stems hirsute-pilose to loosely strigose, petals usually with red lines at base, the lines strong to faint, sometimes absent

3 Stems sparsely to moderately strigose with loosely antrorsely appressed hairs or nearly glabrous, uncommonly sparsely villous proximally, hairs 0.2–0.6 mm, slightly curved, petals mostly 4–8 mm, red lines faint or absent ..... **Oxalis florida**

3 Stems hirsute-pilose on at least proximal 2/3, hairs (0.3–)0.5–1.3 mm, curving, loosely and irregularly spreading, petals 9–20(–23) mm, red lines strongly to weakly evident, occasionally apparently absent

4 Petals (13–)15–20(–23) mm, strongly red-lined, pedicels sparsely villous with long hairs, capsules sparsely to densely hirsute-pilose with long, deflexed, nonseptate hairs, plants strongly colonial; in limestone glades and barrens, chalk prairies, and rocky, limestone habitats **Oxalis macrantha**

4 Petals 9–15 mm, strongly to weakly red-lined or lines occasionally apparently absent, pedicels sparsely closely to loosely strigose with short, upward-arching hairs, capsules nearly glabrous or puberulent to sparsely hirsute-strigose along the angles, plants caespitose or weakly colonial, in a wide variety of habitats ..... **Oxalis colorea**

Other paired-species comparisons

1 Stems glabrous to sparsely and loosely strigose proximally, less commonly villous, with slightly curving, antrorsely oriented hairs 0.2–0.6 mm long, petals mostly 4–8 mm, red lines usually faint or absent; rhizomatous branches and proximal stems herbaceous and slender, without a taproot ..... **Oxalis florida**

1 Stems hirsute-pilose proximally with spreading hairs 0.3–1.3 mm long, petals 9–15 mm, red lines usually strongly evident; rhizomatous branches and proximal stems usually at least slightly lignescent and thickened, taproot often evident ..... **Oxalis colorea**

1 Stems glabrous to sparsely or moderately strigose with loosely antrorsely appressed , slightly curved hairs or nearly distally; capsules nearly glabrous or puberulent to sparsely puberulent along the angles, petals mostly 4–8 mm ..... **Oxalis florida**

1 Stems densely strigose with straight, antrorse, closely appressed, hairs, capsules densely puberulent over the whole surface; petals 6–12 mm ..... **Oxalis dillenii**

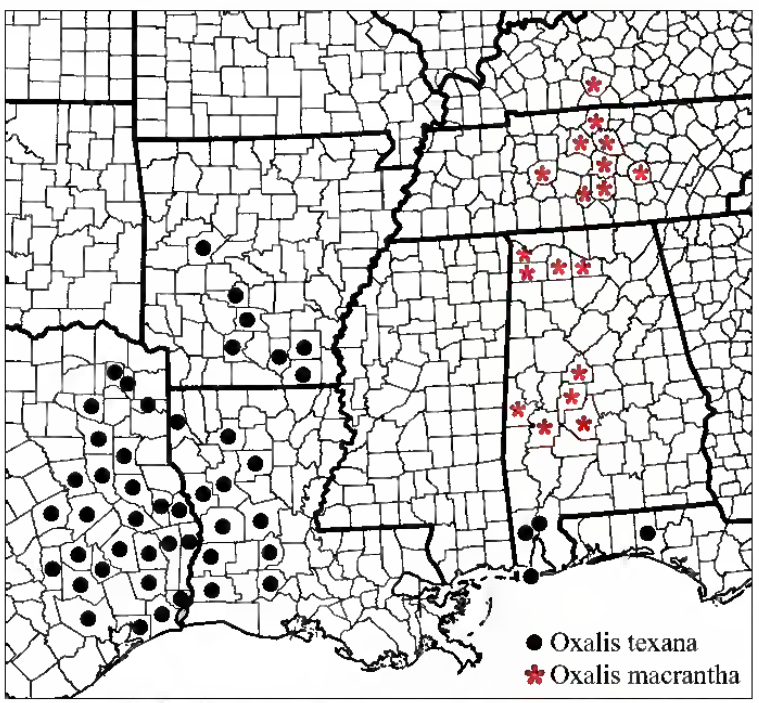

Figure 1. Distribution of *Oxalis texana* and *O. macrantha*. Not shown for *O. texana*, a locality in Goliad Co., Texas, slightly to the southwest.

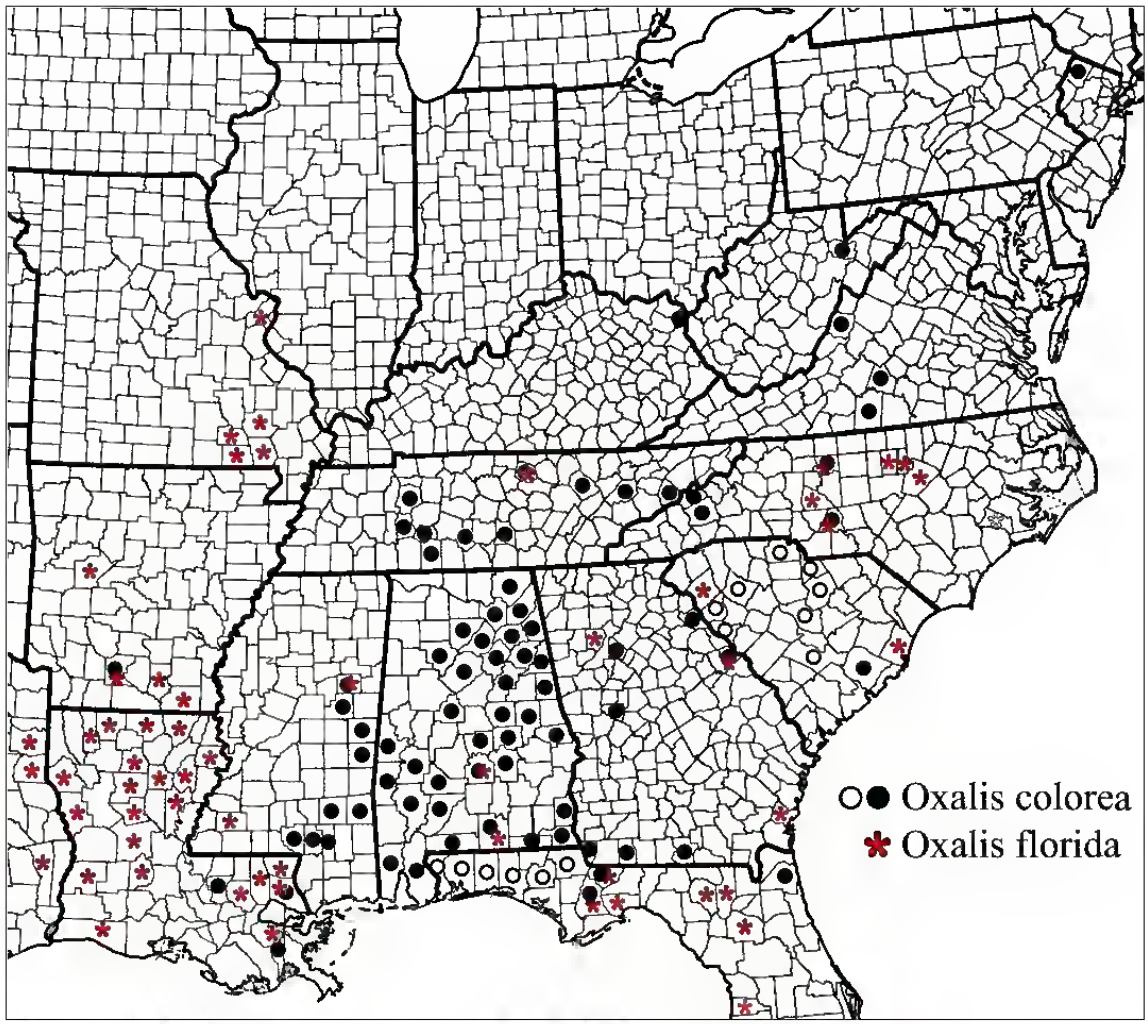

Figure 2. Distribution of *Oxalis colorea* and partial distribution of *O. florida*. Open symbols are from literature, vouchers not seen in the present study (Florida–Ward 2004; South Carolina–SC Atlas 2013). The range of *O. florida* continues south in peninsular Florida (records for Hillsborough, Indian River, Lee, and Manatee counties at MO) and north of North Carolina into New England. Records for *O. florida* in George, South Carolina, and North Carolina are based on study of few collections --- the distribution there probably is much more dense and needs to be studied in detail.

1. OXALIS DILLENII Jacq., Oxalis, 28. 1794. *Oxalis corniculata* var. *dillenii* (Jacq.) Trel. in A. Gray, Syn. Fl. N. Amer. 1(1): 365. 1897. *Xanthoxalis dillenii* (Jacq.) Holub, Bot. Kozlem. 59: 38. 1972. **TYPE**: Jacquin noted in the protologue "Plantam non vidi. Omnia ex Dillenio desumpsi" [Plant not seen. It is entirely selected from Dillenius], thus the name is based on the description and illustration by Dillenius in Hortus Elthamensis 2: f. 298, t. 221. 1732. The plant illustrated probably was raised from seed from a collection made by Mark Catesby, as Sherard and Dillenius had received nearly a full set of Catesby's specimens from eastern North America (Reveal 1983). It apparently is the specimen in Dillenius's herbarium under his phrase-name "Oxys lutea americana, humilior et annua," *Dillenius s.n.* (holotype: OXF).

Oxalis dillenii var. *radicans* Shinners

Oxalis prostrata Haworth; *Oxalis florida* Salisb. subsp. *prostrata* (Haworth) Lourteig

Oxalis lyonii Pursh; *Oxalis corniculata* var. *lyonii* (Pursh) Zucc.

Plants perennial, caulescent, arising from ligneous or lignescent rhizome, sometimes appearing taprootlike. **Stems** usually 2–8 from base, erect initially, 10–25 cm, herbaceous or sometimes becoming lignescent proximally, often becoming decumbent to procumbent and rhizomelike, sometimes rooting at nodes, sometimes proximally lignescent, densely and evenly strigillose to strigose from base to peduncles and pedicels with straight, antrorsely appressed, nonseptate, sharp-pointed hairs. **Leaves** basal and cauline; stipules oblong, margins narrowly flanged or without any free portion, without free apical auricles; petiole 1–4 cm; leaflets 3, green on both surfaces, obcordate, lobed 1/5–1/3 length, (4–)6–15(–21) mm, sparsely strigillose abaxially, glabrous adaxially, oxalate deposits absent. **Peduncles** 1–6(–10) cm. **Flowers** 1 or 2–3(–5, very rarely to 8) in umbelliform (rarely irregular) cymes, mostly homostylous; pedicels in fruit deflexed (to horizontal), usually without bracteoles; sepal apices without tubercles; petals yellow, without red lines, 5–11 mm. **Capsules** angular-columnar, abruptly tapered at apex, 12–20(–25) mm, densely strigose-pilose with mixture of appressed and spreading hairs, with puberulent understory. **Seeds** brownish, transverse ridges with strong grayish or white lines. ***2n*** = 18, 20, 22, 20–24.

Flowering Feb–May(–Oct). Pastures, roadsides, lawns, river bottoms, sandy, rocky, or gravelly soils; 0–300 m; Alta., Man., N.B., N.S., Ont., P.E.I., Que., Sask.; Ala., Ariz., Ark., Colo., Conn., Del., D.C., Fla., Ga., Idaho, Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., Nebr., N.H., N.J., N.Mex., N.Y., N.C., N.Dak., Ohio, Okla., Oreg., Pa., R.I., S.C., S.Dak., Tenn., Tex., Vt., Va., Wash., W.Va., Wis., Wyo.; introduced in Bermuda, Europe.

Oxalis dillenii is highly variable, perhaps polymorphic, especially in habit. A relatively simple and potentially effective approach toward better understanding of the biology would be through a study of chromosome number variation. The geographic range of *O. dillenii* is extensive, apparently completely sympatric with all of the other taxa considered here.

2. OXALIS FLORIDA Salisb., Prodr. Stirp. Chap. Allerton, 322. 1796. **TYPE: USA.** From seeds from South Carolina, probably collected by John Fraser, cultivated in Hortus Chapel Allerton, 1789, *Salisbury s.n.* (holotype: BM digital image!; isotype: G-DC). Fide Lourteig 1979.

Oxalis recurva Ell.; *O. dillenii* subsp. *recurva* (Ell.) C.F. Reed; *O. florida* var. *recurva* (Ell.) H.E. Ahles

Oxalis brittoniae Small

Oxalis filipes Small; *Oxalis dillenii* subsp. *filipes* (Small) Eiten; *Oxalis florida* var. *filipes* (Small) H.E. Ahles; *Xanthoxalis filipes* (Small) Small

Plants perennial, caulescent, arising from very slender stolons or rhizomes, youngest plants apparently beginning from short, slender taproots. **Stems** usually single from base, erect or rarely leaning and decumbent, (5–)8–30(–35) cm, herbaceous, not rooting at nodes, glabrous or subglabrous to sparsely or moderately loosely strigose with fine, slightly curving, antrorsely oriented, non-septate hairs 0.2–0.6 mm, uncommonly sparsely villous proximally. **Leaves** basal and cauline; stipules rudimentary, without free margins or apical auricles; petiole 2–5 cm; leaflets 3, green on both surfaces, obcordate, lobed 1/5–1/3 length, 4–11 mm, sparsely strigose abaxially, oxalate deposits absent. **Peduncles** (2–)3–8 cm. **Flowers** 1 or 2(–3 in umbelliform cymes at level of leaves or slightly above, tristylous; pedicels in fruit reflexing to ascending, often bracteolate; sepals 3.5–5 mm, glabrous, apices without tubercles; petals yellow, sometimes faintly red-lined at base, mostly 4–9 mm. **Capsules** angular-cylindric, 7–10 mm, glabrous or glabrate to sparsely puberulent with short hairs, sometimes only along the angles. **Seeds** all brown, transverse ridges brown. ***2n*** = 16.

Flowering Mar–May(–Aug). Low woods, swamp forests, rich woods, pine woods, sandy sites, burned-over woods, ditches, roadside banks, flood plains, low fields, lake edges, creek banks, pastures, disturbed sites, bluffs, rocky slopes; 10–400 m; Ark., Conn., D.C., Fla., Ga., Ind., Ky., La., Maine, Md., Mass., Miss., Mo., N.H., N.J., N.Y., N.C., Pa., S.C., Tex., Vt., Va., W.Va.

Oxalis florida is recognized by its mostly erect stems, thin stems and peduncles (compared to other species), glabrous to sparsely strigose cauline vestiture of relatively short, slightly and loosely curved hairs, obsolescent stipules, relatively small, and yellow flowers usually without red lines in the throat. It is a species of the Atlantic states and Gulf coast but it also occurs in Texas, Louisiana, southwestern Mississippi, Arkansas, and Missouri, apparently disjunct westward from its main range. The eastern and western expressions of *O. florida* perhaps are different evolutionary entities.

Plants of *Oxalis florida* in the western segment of the range apparently range in habit to more robust than those of the east and often appear to differ from typical *O. dillenii* only in vestiture. The two entities in this region, however, appear to exist in sympatry, occasionally forming intermediates. Observations by George Eiten accompanying labels of *Oxalis florida* from Louisiana: Sabine Parish: "Analysis of mass collection of 43 specimens [*Gregory & Eiten 14a* and *14b*] shows 37 are 'good' O.D. *filpes* (such as the specimens on this sheet), 2 are O.D. *filipes* with possible introgression from O.D. *dillenii*, 3 are O.D. *filipes* with quite certain introgression from O.D. *dillenii*, and 1 plant is good O.D. *dillenii*." Sabine Par.: picnic grounds, side of Rte 171, 5.4 mi N of jct with Rte 6 at Many, 4 Jun 1956, *Gregory & Eiten 14b* (MO). Beauregard Parish: Mass collection [*Gregory & Eiten 27a*] shows 12 plants are 'good' O.D. *filipes*, 1 is good O.D. *dillenii*, and 1 is hybrid between the 2 subspecies." Beauregard Par.: 4 Jun 1956, *Gregory & Eiten 27a* (SMU).

In addition to the records for *Oxalis florida* in Texas shown on Figure 2, plants with greatly reduced cauline vestiture occur in scattered localities through eastern counties (e.g., Harrison, Henderson, Hood, Jasper, Kaufman, Milam, Newton, Robertson, Sabine cos.). These plants, however, produce densely puberulent capsules, in contrast to the sparsely strigose to strigillose or nearly glabrous capsules more characteristic of *O. florida*.

Intermediates apparently occur where the ranges of eastern *Oxalis florida* and *O. colorea* come into contact. For example, *Kral 57346* has large (12 mm), red-lined petals like *O. colorea* but the habit and vestiture of *O. florida*: **Florida**. Gadsden Co.: wooded bluffs of Apalachicola River, S side of Chattahoochee, 18 Mar 1976, *Kral 57346* (MO, VDB). Other plants of intermediate morphology are noted in the comments following *O. colorea*.

Oxalis florida is very abundant in Louisiana (specimens not cited) and probably more abundant in Arkansas than indicated on Figure 2. **Arkansas**. Ashley Co.: Gas line right-of-way and clearcut pine woods W of Ark 133, 2.6 mi S of US 82, S of Crossett, 5 May 1985, *Thomas & Hooks 91822* (NLU). Bradley Co.: Ditch and beside fence, Camp Mansfield access road, 0.6 mi E of the Old Monticello Road, SE of Warren, 23 Nov 1985, *Leslie & Harris 1570* (NLU); Johnsville Prairie 5.9 mi SW of Johnsville on unnamed county road, flat open prairie and sparse woods, 5 Aug 1984, *Thomas et al. 90300* (NLU); along Deer Run Trail in Moro Bay State Park E of Ark 15, 12 Apr 1986, *Thomas & Leslie 95377* (NLU). Ouachita Co.: Clearcut woods on both sides of Ouachita Co. Rd. 545 at Co. Rd. 53, 4 mi SW of Elliott and Ark. 276, 19 Sep 2001, *Thomas & Doffitt 171,788* (NLU). Yell Co.: dry, open, rocky hillsides above Nimrod Dam, Fourche River, Ola P.O., 450 ft, 10 Apr 1941, *Demaree 22653* (MO). **Louisiana**. East Baton Rouge Par.: Baton Rouge, Capitol Heights, 18 Apr 1928, Brown 1908 (SMU). Jefferson Par.: voucher seen but not recorded. St. Tammany Par.: 8.7 mi NE of Covington, silty roadside, 20 Apr 1962, *Shmners 29,633* (SMU). **Mississippi**. Franklin Co.: Homochitto Natl. Forest, disturbed basin of Okhissa Lake site at end of USFS 149, E of US 98 S of Bude, 11 Apr 2003, *Thomas & Havran 173,698* (NLU). **Missouri**. Butler Co.: Poplar Bluff, 14 Aug 1892, *Dewart s.n.* (MO); Mud Creek Natural Area, Mark Twain Natl. Forest, just W of Stoddard Co. line and ca. 2 mi E of Co. Hwy T via dirt road, ca. 7 air mi NE of Poplar Bluff, 370 ft, bottomland oak-hickory forest with occasional swampy areas of *Taxodium*, *Populus*, *Acer*, and *Nyssa*, scattered on muddy banks of stream, 14 Sep 1991, *G. & K. Yatskievych 91-222* (MO). Carter Co.: Grandin, not very common in woods, 6 May 1901, *Bush 363* (MO). Ripley Co.: Doniphan, common in woods, 16

May 1900, *Bush 277* (MO-2 sheets); Pleasant Grove, common in woods, 18 May 1900, *Bush 306* (MO). St. Louis Co.: Ca. 2 mi E of Valley Park, between Meramec River and Marshall Road, near ball park, weedy in open area among grasses, 10 May 1990, *Taylor 5997* (NLU). Wayne Co.: Wappapello Lake State Park, oak hardwood forest and along lake shore, 90 m, 19 May 1999, *Rakotonandrasana et al. 346* (MO). **Texas**. Harrison Co.: Caddo Lake State Park, 12 Apr 1976, *Fleetwood 12135* (BRIT) and *12147* (BRIT). Jasper Co.: ca. 7 mi S of Kirbyville, ca. 2 mi E of Hwy 96, ca. 0.2 mi N of end of unpaved road, wooded uplands, 17 Oct 1977, *Ajilvsgi 5519* (BRIT); 12.5 mi SW of Jasper, edge of water at roadside spring, 10 Oct 1945, *Cory 49826* (SMU). Panola Co.: 12.3 mi SSE of Carthage, sandy stream-bottom woods, 7 Jun 1955, *Shinners 20186* (SMU).

3. OXALIS COLOREA (Small) Fedde, Just's Bot. Jahresber. 32: 410. 1905. *Xanthoxalis colorea* Small, Fl. S.E. U.S. 668, 1333. 1903. *Oxalis priceae* subsp. *colorea* (Small) Eiten, Amer. Midl. Nat. 69: 302. 1963. **TYPE**: **USA. Georgia**. DeKalb Co.: On and about Stone Mt., 100–1500 ft, 1-16 May 1895, *J.K. Small s.n.* (holotype: NY digital image!; isotypes: F, NY digital image!).

Plants perennial, caulescent, arising from a slender lignescent taproot, sometimes with short, lignescent, stoloniform (or offsetlike) rhizomes. **Stems** usually 1–4 from base, mostly erect, 5–15(–25) cm, proximally often lignescent, hirsute-pilose with nonseptate hairs 0.3–1.3 mm long on proximal portion of stem, spreading or slightly deflexed, usually in dissimilar orientations, sometimes loosely antrorsely oriented on peduncles and pedicels. **Leaves** basal and cauline; stipules oblong, with margins narrowly flanged or without any free portion, without free apical auricles; petiole 2–7 cm; leaflets 3, green on both surfaces, obcordate, lobed 1/5–1/3 length, 3–8 mm, sparsely strigose-hirsute on both surfaces, less commonly glabrate, oxalate deposits absent. **Peduncles** (3–)5–10(–15) cm. **Flowers** (1–)2–4(–5) in umbelliform cymes, less commonly irregular cymes, produced well above level of leaves, tristylous (fide Mulcahy 1964); pedicels in fruit deflexed to horizontal, often bracteolate, sometimes branched; sepals 3.5–5 mm, apices without tubercles; petals 9–15 mm, yellow to orange-yellow, with prominent red stripes at base (corolla throat), stripes rarely faint, very rarely apparently absent. **Capsules** angular-cylindric, abruptly tapered at apex, 6–16 mm, glabrous or glabrate to sparsely puberulent with short hairs, sometimes only along the angles or at the apex. **Seeds** brown, usually with white transverse ridges. $2n$ = unknown.

Flowering (Mar–)Apr–May(–Oct). Longleaf pine, longleaf pine-scrub oak, pine-mixed hardwood, hardwood, beech-magnolia, and alluvial woods, shale slopes, sandstone outcrops, granite outcrops, limestone, river and stream banks, hillsides and ridges, bluffs, ravines, clearings, roadsides; 30–300 m; Ala., Fla., Ga., La., Miss., Mo., N.J., N.C., S.C., Tenn., Va., W.Va.

Oxalis colorea is densely distributed in southeastern Mississippi, Alabama, and probably the northern half of Georgia; outliers apparently occur in a wider area toward the north and northeast. Other collections examined. **Arkansas**. Ouachita Co.: Low hills, P.O. Camden, 150 ft, 1 Apr 1938, *Demaree 16789* (MO). **Florida**. Duval Co.: S. Jacksonville, 5 Apr 1897, *Churchill s.n.* (MO). Liberty Co.: Aspalaga, 1898, collector not specified (MO). **Kentucky**. Boyd Co.: Ashland, open, dry banks, 13 May 1935, *Demaree 11313* (SMU). **New Jersey**. Sussex Co.: woods along Flatbrookville-Stillwater Rd., between the Appalachian Trail and Vancampens Brook, open disturbed area, 29 May 1979, *Morton 7719* (VDB). **North Carolina**. [Buncombe Co.:] Asheville, no date, *Ashe 2075* (BRIT, MO); Biltmore, woodlands, 27 May 1898, *Biltmore Herb. 5383a* (MO). Forsyth Co.: Sink Rock, rocky places, 1 May 1934, *Schallert 3651* (SMU). Madison Co.: just E of Tenn. state line on N side of the French Broad River, W of Hot Springs, talus and alluvial woods, 8 May 1976, *Boufford 18107* (MO); RR at Hot Springs, 1 Jun 1899, *Churchill s.n.* (MO). Stanly Co.: near Charlotte, rocky slopes below bluffs of Yadkin River, 20 Apr 1932, *Palmer 39985* (GH, MO); steep moist banks above the Yadkin River, just above the second or lower power dam east of Badin, 10 May 1963, *Wilbur 6826* (GH). **Tennessee**. [Cocke Co.]: Wolf Creek, 28 Jul 1894, *Kearney s.n.* (MO); Wolf Creek, Jul 1894, *Ruth s.n.* (MO); Wolf Creek, dry open woods, Aug 1894 , *Ruth s.n.* (BRIT-2 sheets); near Del Rio,

siliceous bluffs along Newport Rd., 18 Apr 1963, *Sharp et al. 17255* (TENN digital image!). Knox Co.: open woods, Knoxville, Jun 1896, *Ruth s.n.* (MO). Lawrence Co.: ca. 4.5 mi S Rockdale and ca. 1/2 mi E of US 43, sandy clay of oak barren by Staggs Road, 16 May 1973, *Kral 49995* (MO); others from VDB. **Virginia**. Bath Co.: Blackies Hollow, scattered in more open or thinly vegetated openings close to ridgetop, SE side of shale barren spur ridge N of State Rte 629 along (E of) Cowpasture River, 6 km E of Bath Alum, 17 May 1994, *Weboldt 8890* (VDB). Campbell Co.: W of Altavista near Leesville, micaceous road cut, 8 May 1961, *Kral 12274* (VDB). Pittsylvania Co.: Along Banister River 3.3 km downstream from State Rte. 832 bridge, 3 km NE of Motleys Mill and 15 km SW of Mt. Airy, very dry, SE-facing bluff, open hardwood/red cedar canopy, 25 Apr 1995, *Weboldt 9176* (VDB). **West Virginia**. Tucker Co.: Otter Creek Lumber Co., near Hendriks, dry grounds along railroad track, 10 Sep 1904, *Greenman 400* (GH).

Plants of one Mississippi collection from within the geographic range of *Oxalis colorea* have the habit and prominently red-lined petals of *O. colorea*; stem hairs are relatively long but they are antrorsely oriented as in *O. florida*. These plants are considered and mapped here as variants of *O. florida* but they may be better interpreted as populational variants of *O. colorea*. **Mississippi**. Oktibbeha Co.: Botanic Garden of the South, ca. 1.2 mi S of Sessums, S27, NE levee, common, 12 Apr 1992, *McDaniel 31380* (VDB). Similar variation also was encountered, equally rarely, in Alabama and Tennessee. **Alabama**. Covington Co.: Pinelands ca. 5 mi N of Florala on US Hwy 31, 28 Mar 1971, *Kral 41876* (NLU); Lowndes Co.: Blue Bluff at Corps of Engineers' Holy Ground Battlefield Park, S shore of Alabama River, ca. 2 1/4 mi NE of Whitehall, 7 Apr 1982, *Gunn 373* (VDB). **Tennessee**. Jackson Co.: Ca. 5 mi S of Gainesboro, cherty, clay loam of clearing in wooded ravine E of TN 56, 24 Apr 1992, *Kral & Moore 80219* (VDB).

The collection cited above from Forsyth Co., North Carolina, has one plant with distinctive colorea-like stem vestiture but stems of the other four have loosely antrorse hairs.

4. OXALIS MACRANTHA (Trel.) Small, Bull. Torrey Bot. Club 23: 268. 1896. *Oxalis corniculata* var. *macrantha* Trel., Mem. Boston Soc. Nat. Hist. 4: 88, plate 11, fig. 5. 1888. **LECTOTYPE** (Lourteig 1979): **USA**. **Alabama**. No other locality data, no date, *P. Hatch s.n.* (GH!).

Oxalis hirsuticaulis Small, Bull. Torrey Bot. Club 25: 611. 1898.

Oxalis priceae Small, Bull. Torrey Bot. Club 25: 612. 1898; *Xanthoxalis priceae* (Small) Small, Fl. S.E. U.S. 668. 1903.

Plants perennial, caulescent, arising from ligneous or lignescent taproot, usually with numerous, lignescent, stoloniform (or offsetlike) rhizomes rooting at nodes and producing erect stems from nodes. **Stems** usually 2–8 from base, erect or usually becoming decumbent, 5–20(–40) cm, proximally lignescent, hirsute-pilose with nonseptate hairs 0.3–1.3 mm on proximal portion of stem, spreading to slightly deflexed, usually in dissimilar orientations. **Leaves** basal and cauline; stipules oblong, with margins narrowly flanged or without any free portion, without free apical auricles; petiole 2–7 cm; leaflets 3, green on both surfaces, obcordate, lobed 1/5–1/3 length, 4–12 mm, strigose-hirsute on both surfaces, less commonly glabrate, oxalate deposits absent. **Peduncles** (3–)5–10(–15) cm. **Flowers** (1–)3–8 in umbelliform cymes, less commonly irregular cymes, produced well above level of leaves, distylous (fide Mulcahy 1964); pedicels in fruit deflexed to horizontal, often bracteolate; sepals 4–6 mm, apices without tubercles; petals yellow, with prominent red stripes at base (corolla throat), (13–)15–20 mm. **Capsules** angular-cylindric, abruptly tapered at apex, 10–15 mm, moderately to densely hirsute-pilose with long, deflexed, nonseptate hairs, sometimes mostly along the angles. **Seeds** brown, usually with white transverse ridges. $2n$ = unknown.

Flowering Mar–May. Dry limestone glades, cedar barrens, chalk prairies, limestone bluffs and outcrops; 100–250 m; Ala., Ky., Tenn.

Oxalis macrantha is restricted mostly to limestone glades and chalk prairies in Alabama, Tennessee, and Kentucky. It is distinct from the other hirsute-pilose-stemmed plants sympatric with it in those states, the latter identified here as *O. colorea*. Earlier use by Nesom (2009) of the name *Oxalis priceae* Small for this species was incorrect, based on a misinterpretation of the publication data of *O. macrantha*.

5. OXALIS TEXANA (Small) Fedde, Just's Bot. Jahresber. 32: 410. 1905. *Xanthoxalis texana* Small, Fl. S.E. U.S. 667, 1332. 1903. *Oxalis recurva* var. *texana* (Small) Wieg., Rhodora 27: 138. 1925. *Oxalis priceae* subsp. *texana* (Small) Eiten, Amer. Midl. Naturalist 69: 301. 1963. **TYPE: USA. Texas**. Brazoria Co.: Alvin, 20 Apr 1894, *E.N. Plank s.n.* (holotype: NY digital image!).

Plants perennial, caulescent, arising from woody taproot, cespitose with stems arising from caudex or with rhizomelike offsets or stolons rooting at nodes. **Stems** most 2–6, erect to ascending, 5–15 cm, proximally ligneous to lignescent, evenly strigose to strigillose from base to peduncles and pedicels with straight, antrorsely appressed to closely ascending, nonseptate hairs. **Leaves** basal and cauline; stipules oblong, usually with margins very narrowly flanged, usually with rounded and slightly free apical auricles; petiole 2–6 cm; leaflets 3, green to purple on both surfaces, cordate, lobed 1/5–1/3 length, (4–)6–12(–18) mm, sparsely strigose abaxially, glabrous to sparsely strigose adaxially, oxalate deposits absent. **Peduncles** 4–10 cm. **Flowers** (2–)3–5(–8) in umbelliform cymes, very rarely irregular cymes, distylous; pedicels in fruit horizontal to deflexed, without bracteoles; sepal apices without tubercles; petals yellow, with prominent red lines at base (corolla throat), (10–)12–16(–17) mm. **Capsules** angular-columnar, abruptly tapered at apex, 8–15 mm, moderately to densely puberulent to puberulent-villous. **Seeds** brownish, transverse ridges distinctly whitish. $2n$ = unknown.

Flowering Mar–May(–Jun). Commonly in undisturbed habitats and usually in deep, loose sand, but also fields, roadsides, and edges and openings in woods, pine, pine-oak, and mixed hardwoods; 10–200 m; Ala., Ark., Fla., La., Tex.

Representative collections examined. **Arkansas**. Bradley Co.: Warren, prairie, 200 ft, 10 Apr 1943, *Demaree 24233* (SMU). Dallas Co.: 2.6 mi WSW of Fordyce, roadway in pine-oak woods, fine sandy clay, 1 May 1955, *Shinners 19892* (SMU). Drew Co.: Monticello, ridge, pine woods, 10 Apr 1937, *Demaree 14374* (SMU); Monticello, ridge thickets, 250 ft, 26 Mar 1938, *Demaree 16738* (SMU). Hot Springs Co.: Magnet Cove, low hills, 550 ft, 18 Apr 1937, *Demaree 14564* (SMU); Magnet Cove, rocky limestone hills, 550 ft, 2 May 1937, *Hale 220* (VDB). Marion Co.: 18 mi W of Yellville, along road and wooded hillside, 15 Apr 1976, *Lipscomb 1254* (BRIT). **Louisiana**. Numerous collections from Acadia, Beauregard, Bienville, Calcasieu, Evangeline, Natchitoches, Rapides, Sabine, and Vernon parishes. **Texas**. Collections studied from TEX-LL, BRIT-SMU, MO, NLU.

Nesom (2009), following Eiten (1963), cited a collection (*Ewan 17608*) from Rapides Parish, La., as *Oxalis priceae*, (interpreted here now as *O. colorea*) but recent field observations in Rapides Par. show that populations of *O. texana* (e.g., *Nesom 2013-1*, cited below) occasionally produce individuals with a tendency for stem hairs to be spreading on proximal portions. Otherwise, all have closely antrorsely appressed stem hairs characteristic of *O. texana*. **Louisiana**. Rapides Par.: Red River valley, near Zimmerman RR Sta., frequent in dryer spots beneath tall pines on crest of hills, 24 Apr 1948, *Ewan 17608* (MO); Kisatchie Natl. Forest, ca. 15 air mi SW of Alexandria center, ca. 10 air mi SSW of Alexandria Interntl. Airport, jct La. Hwy 488 and FS Road 240 to USAF Claiborne Bombing Range at N side of range area, recently controlled-burn area (probably in 2011 or 2012), loblolly pine emphasis with mixed oak-hickory and sassafras, gentle slopes, sandy soil, elev. 225 ft, with *Pteridium aquilinum*, *Rhus copallina*, *Rhus toxicodendron*, *Oxalis violacea*, *Glandularia*

canadensis, *Hypoxis*, *Tephrosia*, *Pityopsis*; locally common within woods but not along roadsides or in other disturbances, 27 Apr 2013, *Nesom 2013-1* (BRIT, and to be distributed).

The Alabama plants identified here as *Oxalis texana* all are from Dauphin Island and localities in and around Mobile (Fig. 1). Only a single collection has been seen from Florida. Compared to those in Texas and Louisiana, these more eastern plants have shorter petals (6–12 mm vs. (10–)12–16(–17) mm long), a more colonial habit (taprooted, usually with long, lateral, rhizome-like branches vs. taprooted, commonly with short basal offsets), and they grow in disturbed sites (vs. mostly undisturbed sites, usually within woods). It is plausible that they may prove to be more closely related to *O. colorea* than to the more western *O. texana*. Orientation of cauline vestiture is weighted in the identification here of the Alabama plants.

Specimens examined. **Alabama**. Baldwin Co.: weedy along disturbed roadside on E side of Hwy 225, ca. 0.3 mi S of Dennis Creek, 18 Mar 2012, *Horne 1748* (AMAL). Mobile Co.: Dauphin Island, dry sunny roadside ditch near ine forest, 9 May 1964, *Deramus D60* (BRIT); Dauphin Island, common in sandy soils of relatively open, weedy lawn at 710 Cadillac Avenue, 4 Mar 2012, *Horne 1733* (AMAL); Dauphin Island, open lawn of residence at 722 Cadillac Avenue, ca. 500 ft W of Horne 1733, 4 Mar 2012, *Horne 1735* (AMAL); Dauphin Island, weedy lawn around island's water tower directly S of the 3-way stop intersection of Bienville Blvd. and LeMoyne Drive (Hwy 193), 10 Mar 2012, *Horne 1737* (AMAL); Alabama State Park Authority property, weedy along edge of small dirt parking lot at Entrance B of the Mud Lakes Disposal Area on the E side of Hwy 90 near the S end of the Cochrane Bridge over the Mobile River, 17 Mar 2012, *Horne 1740* (AMAL); Dauphin Island, Audubon Bird Sanctuary, shaded understory of mesic maritime woods along trail leading from parking lot to Banding Area, 7 Mar 2012, *Horne 1744* (AMAL); Mobile, common around Rochelle's Diner at 2904 Spring Hill Ave, 19 Mar 2012, *Horne 1751* (AMAL); Mobile, weedy along disturbed western edge of parking lot for B.A. Vitter & Assoc., 8060 Cottage Hill Rd, 19 Mar 2012, *Horne 1752* (AMAL, BRIT); Dauphin Island, mesic coastal pine forest of Audubon Bird Sanctuary along trail leading from parking lot to Banding Area, 2 Apr 2012, *Horne 1757* (AMAL); Dauphin Island, open, grassy roadside on S side of Infanta Place, ca. 100 ft E of its intersection with Iberville Drive, 10 Feb 2013, *Horne 1975* (BRIT); Dauphin Island, pine woods near water tower, 25 Mar 1973, *Taylor 12746* (BRIT). **Florida**. Walton Co.: Four Mile Village area of Coffeen Nature Preserve, S of Hwy 98, E of Sandestin, frequent in sand of interdune swales, 4 Mar 1990, *Anderson 12575* (MO).

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Nesom, G.L. 2014. *Oxalis pilosa* (Oxaliidaceae) adventive in Texas. Phytoneuron 2014-13: 1–3. Published 6 January 2014. ISSN 2153 733X

OXALIS PILOSA (OXALIDACEAE) ADVENTIVE IN TEXAS

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ABSTRACT

Oxalis pilosa was observed and collected in a park in San Angelo, Texas (Tom Green Co.), in 1983, where it apparently was naturalized. The Texas locality is long-disjunct from the primary range of the species far to the west.

Continued study of *Oxalis* collections reveals the presence in Texas of *O. pilosa* Nutt. ex Torr. & A. Gray, a species not previously known to occur in the state. It is known only from this single collection, disjunct far to the east of its primary geographic range.

Voucher. **Texas**. Tom Green Co.: South San Angelo, dry sandy soil S of Southland Park, 14 Mar 1983, *Steen 12* (BRIT). Figures 1 and 2.

The native distribution of *Oxalis pilosa* is primarily in Arizona, southern California, and northwestern Mexico — it occurs as an adventive in peripheral localities in Nevada, New Mexico, Oregon, and Utah (Nesom 2009). In Mexico it occurs primarily in northwestern states (Baja California, Chihuahua, Coahuila, Durango, Sonora), with scattered localities to the east in Nuevo León.

Oxalis pilosa is characterized as a caulescent perennial arising from a ligneous or lignescent taproot. Stems are proximally lignescent, usually 2–8 from the base, decumbent to ascending, and sparsely to densely pilose, the hairs spreading, irregularly oriented to somewhat regularly deflexed, the longer 0.7–1.2 mm. It has been treated as an infraspecific entity within *O. albicans*, but the two are sympatric in the southwestern USA and although each is variable, there appear to be relatively few unequivocal intermediates.

1. Stems sparsely to densely pilose, hairs spreading, irregularly oriented to somewhat regularly deflexed, longer hairs mostly 0.7–1.2 mm, midstem stipules with very narrow, free margins ..... **Oxalis pilosa**
1. Stems puberulent to hirsutulous-puberulent, hairs usually upcurved or crisped, sometimes straighter, longer hairs 0.2–0.3(–0.8) mm; midstem stipules obsolescent or with very narrow, free margins ..... **Oxalis albicans**

Oxalis albicans subsp. *pilosa* (Nutt. ex Torr. & A. Gray) Eiten
Oxalis corniculata subsp. *pilosa* (Nutt. ex Torr. & A. Gray) Lourteig
Oxalis corniculata var. *pilosa* (Nutt. ex Torr. & A. Gray) B.L. Turner
Oxalis wrightii A. Gray var. *pilosa* (Nutt. ex Torr. & A. Gray) Wieg.

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Nesom, G.L. 2009. Notes on *Oxalis* sect. *Corniculatae* (Oxalidaceae) in the southwestern United States. Phytologia 91: 527–533.

Figure 1. *Oxalis pilosa* from Tom Green County, Texas.

Figure 2. Densely deflexed-pilose cauline vestiture of *Oxalis pilosa* from Tom Green Co., Texas.

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CASTILLEJA COCCINEA AND *C. INDIVISA* (OROBANCHACEAE)

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ABSTRACT

Castilleja coccinea and *C. indivisa* are contrasted in morphology and their ranges mapped in detail in the southern USA, where they are natively sympatric in small areas of Oklahoma, Arkansas, and Louisiana. *Castilleja indivisa* has recently been introduced and naturalized in the floras of Alabama and Florida. *Castilleja ludoviciana*, known only by the type collection from southwestern Louisiana, differs from *C. coccinea* in subentire leaves and relatively small flowers and is perhaps a population introgressed by *C. indivisa*.

Castilleja coccinea and *C. indivisa* are allopatric except in small areas of Oklahoma, Arkansas, and Lousiana, but assessments of their native distributions are not consistent among various accounts (e.g. Thomas & Allen 1997; Turner et al. 2003; OVPD 2012; USDA, NRCS 2013). Morphological contrasts between the two species, via keys in floristic treatments (e.g., Smith 1994; Wunderlin & Hansen 2003; Nelson 2009; Weakley 2012), have essentially repeated the differences outlined by Pennell (1935). The current study presents an evaluation and summary of the taxonomy of these two species.

We have examined specimens at CAS, TEX-LL, SMU-BRIT-VDB, MO, NLU, NO, USF, WS, and WTU and viewed digital images available through Florida herbaria and databases.

CASTILLEJA COCCINEA (L.) Spreng., Syst. Veg. 2: 775. 1825. *Bartsia coccinea* L., Sp. Pl. 2: 602. 1753. *Euchroma coccinea* (L.) Nutt., Gen. N. Amer. Pl. 2: 54. 1818. **LECTOTYPE**: (Jarvis 2007): **USA. Virginia**. No other collection data, *J. Clayton 293* (BM digital image!).

Castilleja coccinea forma *alba* Farwell, Amer. Midl. Naturalist 8: 276. 1923. **TYPE**: **USA. Michigan**. Oakland Co.: Goodison, 6 Jun 1923, *O.A. Farwell 6507* (BLH digital image!).

Castilleja coccinea forma *lutescens* Farwell, Amer. Midl. Naturalist 8: 276. 1923. **TYPE**: **USA. Michigan**. Oakland Co.: Goodison, 6 Jun 1923, *O.A. Farwell 6506* (BLH digital image!).

Castilleja coccinea forma *pallens* (Michx.) Pennell, Monogr. Acad. Nat. Sci. Philad. 1: 535. 1935. *Bartsia coccinea* var. *pallens* Michx., Fl. Bor.-Amer. 2: 17. 1803. **TYPE**: No type specified in protologue. "Bracteis lutescentibus. Rarior." Pennell cited the authorship of the original name as "Pursh, Fl. Amer. Sept. 429. 1814" and assumed that the name was intended at the rank of forma, but Pursh merely repeated the earlier phrasing of Michaux.

Castilleja ludoviciana Pennell, Monogr. Acad. Nat. Sci. Philad. 1: 540. 1935. **TYPE**: **USA. Louisiana**. Jeff Davis Par.: Low prairies, Welsh, 17 May 1915, *E.J. Palmer 7656* (holotype: MO! digital image!, Fig. 1; isotypes: CAS!, PH, US!, WS!). Annotated as *Castilleja coccinea* by K.A. Vincent in 1981.

Annual herbs, fibrous-rooted. **Stems** erect, 12–50 cm, usually unbranched, short villous with fine, eglandular hairs and much shorter, glandular hairs. **Leaves**: cauline oblong-lanceolate to narrowly oblong-lanceolate or linear-lanceolate, 2–7 cm, never subclasping, consistently with 1–3 approximately paired, linear to narrowly lanceolate lobes (2–)5–25 mm, rarely entire (e.g., Louisiana, Minnesota); basal in persistent rosette though often withered at anthesis, oblanceolate to oblong-lanceolate, 1–3 cm, unlobed, discontinuous in morphology from the cauline; surfaces of basal and cauline hirsutulous-puberulent. **Inflorescence** spicate, unbranched, 3–35 cm (longest in fruit), proximal internodes 2–4.5 cm in fruit. **Bracts** 14–22 mm, proximal lanceolate with 3 lanceolate lobes, apices acute, all green, distally becoming obovate in outline and shorter, 3-lobed divided ca. 1/2 the bract length, or the middle lobe sometimes with 1–2 short lateral lobes, distally red (rarely yellow), apices acute to obtuse. **Flowers** sessile to subsessile; calyces 17–28 mm, divided 1/3–1/2; corollas 18–25 mm, usually exserted 3–7 mm beyond the calyx apex, galea 8–10 mm, 1/4–1/3 length of the tube, greenish with thin, yellowish margins, teeth 2–4(–5) mm, green to yellowish, apically pink to yellow; stigma exserted. **Seed coat** shallowly foveolate-reticulate.

Flowering Apr–Jun(–Jul). Low meadows and fields, ditch and swamp edges, bogs, prairies, roadsides, beach ridges and dunes, jack pine plains, rocky woodlands, sandstone outcrops, limestone ledges, granite cliffs; 150–3300(–4100) ft; Ala., Ark., Conn., Del., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.H., N.J., N.Y., N.C., Ohio, Okla., Penn., R.I., S.C., Tenn., Va., Wis., W.Va.; Man., N.S., Ont., Sask.

Yellow-bracted plants (*Castilleja coccinea* forma *lutescens* Farwell), otherwise similar to the species in its regional expression, occur sporadically over the range of the species (e.g., Arkansas–Izard Co.; Illinois–Lake Co.; Indiana–Pulaski Co., Starke Co.; Michigan–Cass Co., Oakland Co.; Minnesota–Morrison Co.; Oklahoma–Cherokee Co., Ottawa Co.).

Occurrences of *Castilleja coccinea* in Louisiana (Fig. 2) are documented by these collections: Calcasieu Par.: Lake Charles, prairies, 2 Apr 1911, *R.S. Cocks s.n.* (NO). Jeff Davis Par.: Welsh, prairies, 28 Mar 1906, *R.S. Cocks s.n.* (NO). Jeff Davis Par.: Welsh, low prairies, 17 May 1915, *E.J. Palmer 7656*, the type of *C. ludoviciana*. Rapides Par.: Alexandria, no date, *J. Hale s.n.* (NO, fide Pennell 1935). In Texas the only bona fide record for *C. coccinea* is from Bowie County, as documented by Singhurst et al. (2011).

Pennell (1935) described *Castilleja ludoviciana* as a species and distinguished it and *C. coccinea* as a pair from *C. indivisa* by the following contrasts (p. 535).

1. Lower lip of corolla very short, thickened, green; corolla 20–25 mm long; leaf blades entire or slightly lobed; basal rosettes not or scarcely formed, certainly not persisting until anthesis ..... **Castilleja indivisa**
1. Lower lip of corolla more developed, distally thin and yellowish; basal leaf rosettes more or less evident.
   2. Corolla 20–25 mm long, the lower lip less than 1/3 length of galea; cauline leaf blades pinnately lobed; basal leaf rosettes well-developed, persisting until after anthesis ..... **Castilleja coccinea**
   2. Corolla 13–15 mm long, the lower lip about 1/2 length of galea; cauline leaf blades entire or nearly so; basal rosettes less developed, scarcely evident at anthesis ..... **Castilleja ludoviciana**

We confirm the distinction of *Castilleja indivisa* in generally the same features, particularly leaf morphology and arrangement. As noted by Pennell, the lower corolla lip is relatively shorter in *C. indivisa* but the morphology of the lip in *C. coccinea* apparently is more variable than he surmised.

Figure 1. *Castilleja ludoviciana* Pennell, holotype (MO).

The collection described by Pennell as *Castilleja ludoviciana* was made from southwestern Louisiana (Fig. 2), where *C. coccinea* and *C. indivisa* are sympatric in native range, at least historically. The entire-margined cauline leaves of *C. ludoviciana* and the short calyces (14–15 mm) and corollas (13–15 mm), as recorded by Pennell and confirmed here in study of the holotype and isotypes, distinguish it from *C. coccinea*.

Most of the features of *Castilleja ludoviciana* (Fig. 1) are within the range of variation of *C. coccinea* — the cauline leaves are not clasping and the basal leaves of *C. ludoviciana* are the same as those found in many populations of typical *C. coccinea*, where they vary in persistence in an unwithered condition. In *C. ludoviciana* and commonly across the range of *C. coccinea*, the basal leaves are somewhat withered but mostly persistent and still morphologically distinct from the cauline. Lobed-leaf individuals occur commonly as population variants throughout the range of *C. indivisa*, but apart from *C. ludoviciana*, entire-leaved variants apparently do not occur in *C. coccinea*.

The entire leaves of *C. ludoviciana*, suggest that it may be a variant of *C. coccinea* showing genetic influence of *C. indivisa*, especially since *C. ludoviciana* lies within the range of *C. coccinea* in an area where *C. indivisa* also occurs (both species as natives in southwestern Louisiana are rare, perhaps extinct, see comments and specimen citations above and below), and a collection of typical *C. coccinea* was made very near the 'ludoviciana' locality. Possible interspecific hybrids between *C. coccinea* and *C. indivisa* might also be sought in eastern Oklahoma and northwestern Arkansas, where the two also are sympatric.

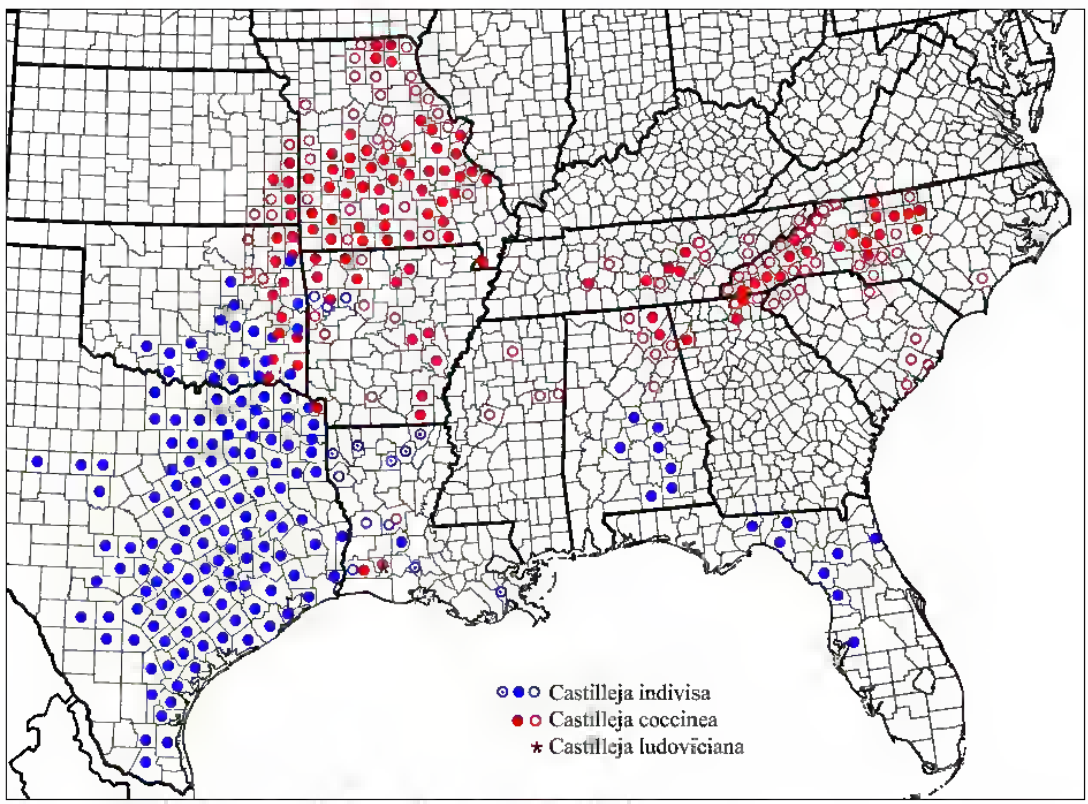

Figure 2. Distribution of *Castilleja coccinea* and *C. indivisa* in south-central and southeastern states of the USA. The distribution of *C. coccinea* continues northward into Canada. Solid symbols are from collections examined; open symbols are from literature and internet sources; dotted symbols (Louisiana) are collections examined from cultivation or immediate garden escapes or from along roadsides where probably seeded for cultivation.

In the present study, *Castilleja coccinea* and *C. indivisa* are distinguished by the following contrasts.

1. Cauline leaves never subclasping, consistently 1–3-lobed, rarely entire (*C. ludoviciana*), basal in a persistent rosette though often withered at anthesis, oblanceolate to oblong-lanceolate, unlobed, discontinuous in morphology from the cauline ..... **Castilleja coccinea**
1 Cauline leaves often subclasping, entire or less commonly 1–2(–3)-lobed (variants scattered through range of the species), basal/lower cauline not forming a distinct rosette but sometimes relatively dense on short internodes, similar in morphology to more distal cauline ..... **Castilleja indivisa**

CASTILLEJA INDIVISA Engelm., Boston J. Nat. Hist. 5: 255. 1845. **TYPE: USA. Texas**. Prairies from Houston to the Colorado, 1844, *F. Lindheimer 284* (holotype: MO 88172! digital image!; isotypes: CGE!, E!, GH!, K-BENTH, K-HOOK!, MO 88171! and 88186! digital images!, PH!, US!).

Castilleja indivisa forma *vivida* Cory, Field & Lab. 17: 65. 1949. **TYPE: USA. Texas**. Refugio Co.: 9 3/4 mi SW of Woodsboro, sandy bank of roadside cut, 28 Mar 1948, *V.L. Cory 54158* (holotype: SMU!).

Annual herbs, fibrous-rooted to nearly taprooted. **Stems** erect, 1(–3) from the base, usually unbranched or with 1–3 branches from the proximal half, (5–)10–45 cm, short villous with fine, eglandular hairs and much shorter, glandular hairs. **Leaves** narrowly lanceolate to linear-lanceolate, 2–8(–9) cm, not forming a distinct basal rosette, sometimes relatively dense proximally on short internodes but similar in size and shape to more distal cauline, sessile, often subclasping, entire or less commonly with 1–2(–3) approximately paired, linear to filiform lobes 1–20 mm, surfaces hirsutulous-puberulent. **Inflorescence** spicate, unbranched, 2–16(–20) cm, villous with fine, eglandular hairs. **Bracts** 5–25 mm, proximal lanceolate-acuminate with acute apices, all green, distally abruptly becoming shorter and obovate to broadly obovate or obtrullate and with rounded to obtuse apices, distal 2/3 scarlet to crimson or salmon pink (rarely white to yellowish), unlobed. **Flowers** sessile to subsessile; calyces 16–22 mm, divided 1/4–1/3 length, primary lobes 6–9 mm, distally red to pink (rarely white to yellowish); corollas (15–)17–24 mm, equal to calyx or exserted 1–6 mm beyond the calyx apex, galea 4–9 mm, ca. 1/5 length of the tube, dorsally yellow to pink, glandular-puberulent, teeth of lower lip 0.5–2 mm, green, thickened, white to yellowish; stigmas exserted, capitate. **Seed coat** shallowly foveolate-reticulate.

Flowering (Mar–)Apr–May(–Jul). Grasslands, blackland prairie, limestone rocky slopes and glades, shell ridges, sandhills, dunes, pastures, old fields, roadsides and ditches, sand and sandy loam, red clay, juniper, oak-juniper, pine, post oak, mesquite-hackberry woodlands; 20–1200 ft; Ala., Ark., Fla., La., Okla., Tex.; Mexico (Aguascalientes, Chihuahua).

As in *Castilleja coccinea*, yellow-bracted individuals of *C. indivisa*, apparently within otherwise red-bracted populations, are scattered over its range (e.g., Brazos, Red River, Travis, Victora, Wharton counties, Texas). Lobed-leaf variants at least in some cases may reflect introgression from the *C. purpurea* complex (Nesom & Egger 2014).

An enclave of uniformly white-bracted populations occurs in a small area of Nueces Co., Texas, between Aransas Pass and Port Aransas. **Vouchers**: N side of TX 361 on Stedman Island, 1.3 mi ESE of RR crossing on E edge of city of Aransas Pass, common in dredged, probably saline sand, silt and roadbase, grassy roadside, floral parts white in all plants, 4 Mar 1992, *Carr 11714* (TEX); sandy flats on Stedman Island ca. 1 mi ESE of Aransas Pass, 11 Mar 1977, *Duncan 30402* (VDB); along causeway between Aransas Pass and Port Aransas, local populations all white-flowered, scattered, 18 Mar 1996, *Fryxell 5062* (TEX); shell and sand reef between Aransas Pass and Port Aransas, 21 Apr 1935, *Goldsmith s.n.* (PH fide Pennell 1935, TEX); S side of FM 361 at E end of bridge over Redfish Bay enroute to Port Aransas from Aransas Pass, 19 Apr 1988, *Jones 1116* (TAES). A case might be made for the formal taxonomic recognition of this population system.

The northernmost record of *Castilleja indivisa* apparently is a collection for which locality data are minimal: **Oklahoma**. Meadow near Kansas, 2 May 1925, *Small & Wherry 12228* (TEX). A collection of *C. coccinea* was made at the same locality and date: *Small & Wherry 12239* (TEX). Original identifications of both species were correct. Presumably the collections were made from one of the northeastern counties bordering Kansas (Washington, Nowata, Craig, Ottawa), where *C. coccinea* is known from other collections, but the *C. indivisa* record is not mapped in Figure 2.

The only Louisiana collection encountered in this study of *Castilleja indivisa* that apparently occurred in a natural habitat is this: Evangeline Par.: deciduous woods in Chico State Park, ca. 4 mi N of Ville Platte, 3 Apr 1981, *Givens 1961* (NLU). All other collections from Louisiana (Fig. 2) are from explicitly cultivated plants, plants clearly immediately escaped from garden cultivation, or plants recently collected along roadsides of major highways where they probably were seeded as part of wildflower mixes. All Louisiana collections of *C. indivisa* seen in this study were made from 1978 to 1988.

Castilleja indivisa has recently been introduced and is becoming abundant in parts of Alabama and Florida (Fig. 2), disjunct eastward from its main range. Alabama collections all have been from roadsides; the earliest was made in 1995. Florida collections are from roadsides and roadside ditches; the earliest were made in Taylor Co. (1961) and Levy Co. (1991). A 1998 collection from Madison Co., Florida, specifically notes that there were "Large planted colonies on the N side of the interstate and in the median."

Two collections from Mexico are identified here as *Castilleja indivisa*, apparently representing instances of long disjunction, presumably through seeds carried either by wind or by vehicles. **Aguascalientes**. Mpio. San José de Gracia, 12 km SW of La Congoja, ladera riolitica con veg. de bosque abierto de *Quercus*, *Pinus*, y *Juniperus*, 2700 m, 16-17 Oct 1973, *Rzedowski & McVaugh 746* (MICH). **Chihuahua**. SW of Colonia Juárez, near Nuevo Casas Grandes, dry slopes in scrub area, 3 Aug 1965, *Melchert 351* (IA).

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REVIEW OF THE *CASTILLEJA PURPUREA* COMPLEX (OROBANCHACEAE)

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ABSTRACT

Since 1958, the purple-bracted *Castilleja purpurea* has been treated to include the yellow-bracted *C. citrina* (as *C. purpurea* var. *citrina*) and the red- to orange-bracted *C. lindheimeri* (as *C. purpurea* var. *lindheimeri*). It is proposed here that each of the three be treated at specific rank, emphasizing their largely consistent morphology, the relatively narrow zones of hybridization along areas of contact, compared to the much larger areas within which each of the three is consistent, and the consistent distinction between *C. citrina* and *C. purpurea* even within a significant area of sympatry. *Castilleja purpurea* and *C. citrina* in the northern part of their ranges (Kansas, Oklahoma, Missouri) are allopatric, while in central Texas they are sympatric. The region of sympatry is characterized by a mix of populations of typical morphology and populations of variable bract and calyx color — sympatric populations of *C. citrina* are considerably less variable than any of *C. purpurea*. *Castilleja lindheimeri* is parapatric to narrowly sympatric with both *C. purpurea* and *C. citrina* and morphologically distinct from both, although some hybrids occur. A biologically appropriate taxonomy of most populations of the *C. purpurea* complex is possible with identifications of *C. purpurea*, *C. citrina*, and *C. lindheimeri*, for intergrades using *C. purpurea*< >*citrina*, *C. purpurea*< >*lindheimeri*, and *C. lindheimeri*< >*citrina*, or simply "*C. purpurea* complex intergrade."

Castilleja purpurea (Nutt.) G. Don and *C. lindheimeri* A. Gray were early described from collections of early explorers. After traveling and observing in Texas, Pennell (1935) added *C. citrina* Pennell as well as two other Texas paintbrush species he considered to be narrow endemics. Lloyd Shinners moved to Texas in 1945, and after becoming familiar with the flora of central Texas, probably upon seeing variable populations in north-central counties, he reckoned that the whole *C. purpurea* complex was best conceptualized as a single species (1958). His nomenclatural combinations were not accompanied by any explanatory comment. Since the precedent by Shinners, floristic accounts and studies have followed in recognizing *C. purpurea* with three varieties (e.g., Holmgren 1970; Great Plains Flora Association 1986; Nesom 1992; Diggs et al. 1999; Turner et al. 2003; Nelson 2009).

In 2013, with the advantage of having a large number of collections at hand to study, with personal paintbrush experience in the field by both authors, and with the opportunity to review the *Castilleja purpurea* complex in connection with preparation of the FNA *Castilleja* treatment, we offer an alternative point of view. Many questions arise in relation to whatever taxonomic approach is taken, and we hope that the underlying biology of these plants will become better understood. The hypothesis guiding the nomenclature presented here can be tested in various ways.

Observations pertinent to the taxonomic interpretation follow below, with a formal presentation of the nomenclature. The distribution map (Fig. 1), which summarizes information

critical to our interpretation, is derived mostly from specimens examined at TEX-LL, BRIT-SMU-VDB, BAYLU, TAES-TAMU, NLU, and MO. All photos are by Egger.

Typical forms and variants

Over most of their geographic ranges, and even in areas of sympatry, *Castilleja citrina* (yellow inflorescence; Figs. 4, 6, 7), *C. purpurea* (purple inflorescence; Figs. 2, 3), and *C. lindheimeri* (red inflorescence; Figs. 10, 11) occur in populations of relatively narrow variation in bract and calyx color. Color differences among the three imply that isolating mechanisms may involve differences in pollinators. Introgression appears to be limited in geographical extent, but widely variable populations are conspicuous and occur mostly along zones where ranges are in close contact (Fig. 1). Populational variants from pinkish purple to red, reddish orange, burnt orange, pink, peach, light yellow, creamy (very light orange-yellow), and rarely white have been observed.

Castilleja citrina and *C. purpurea* are allopatric in Kansas and most of Oklahoma, but they are partially sympatric in north-central Texas and into southeastern Oklahoma. Typical populations of purple-bracted *C. purpurea* exist in the area of sympatry, and many sympatric populations of *C. citrina* also are consistent in morphology, the plants identifiable by their yellow bracts and calyces and large, yellow, thin-petaloid lower corolla lips. Some observations suggest that gene flow is mostly unidirectional from *Castilleja citrina* into *C. purpurea*. "Populations of [*C. citrina*] are considerably less variable in coloration than in the other two [taxa]. ... Genes of [*C. citrina*] apparently are present in populations of [*C. purpurea*] in their region of contact, but not vice versa, as if [*C. citrina*] were serving only as the pollen parent of the putative hybrids" (Nesom 1992, p. 216–217).

Castilleja citrina and *C. lindheimeri* are parapatric or narrowly sympatric in south-central Texas counties (Fig. 1), mostly away from the range of *C. purpurea*, and little evidence of intergradation between them is evident in herbarium collections. Hybridization probably does occur, however, as indicated by an orangish yellow plant from Gillespie County (Fig. 9), where only *C. citrina* and *C. lindheimeri* occur.

Castilleja lindheimeri and *C. purpurea* are parapatric or narrowly sympatric (Fig. 1). Each apparently maintains a consistent morphology except immediately along the area of contact (e.g., in Coleman Co., Fig. 5). A set of vouchers was made from a population "between highway [317] and railway" in McLennan County (4 Apr 1949, *Cory 55470* a, b, c, d, e, and f, SMU), where only *C. lindheimeri* and *C. purpurea* occur, with the label observation that the population included six color forms (all apparently mostly red to pink or purplish).

Pennell (1935) cited as *Castilleja lindheimeri* a few collections from counties within the geographic range of *C. purpurea* but outside that of *C. lindheimeri* (e.g., Comanche, Eastland, Erath, Menard, Mills, Parker, Stephens). This probably reflects the difficulty in determining color of calyces and bracts in specimens that were not dried quickly in preparation or with color faded in age. Recent collections, especially those where inflorescence color is noted in the collection data, support the distinction in geography between *C. lindheimeri* and *C. purpurea*, as mapped in Figure 1.

One species or three?

The three entities of the *Castilleja purpurea* complex are differentiated mostly in the color of bracts and calyces. Putative differences in corolla and calyx sizes noted by Pennell (1931) do not appear to be consistent. The distinctively large, petaloid, lower corolla lip of *C. citrina* noted by Pennell and others is generally consistent and diagnostic, but lips of similar morphology (except in color) sometimes also occur in *C. purpurea*.

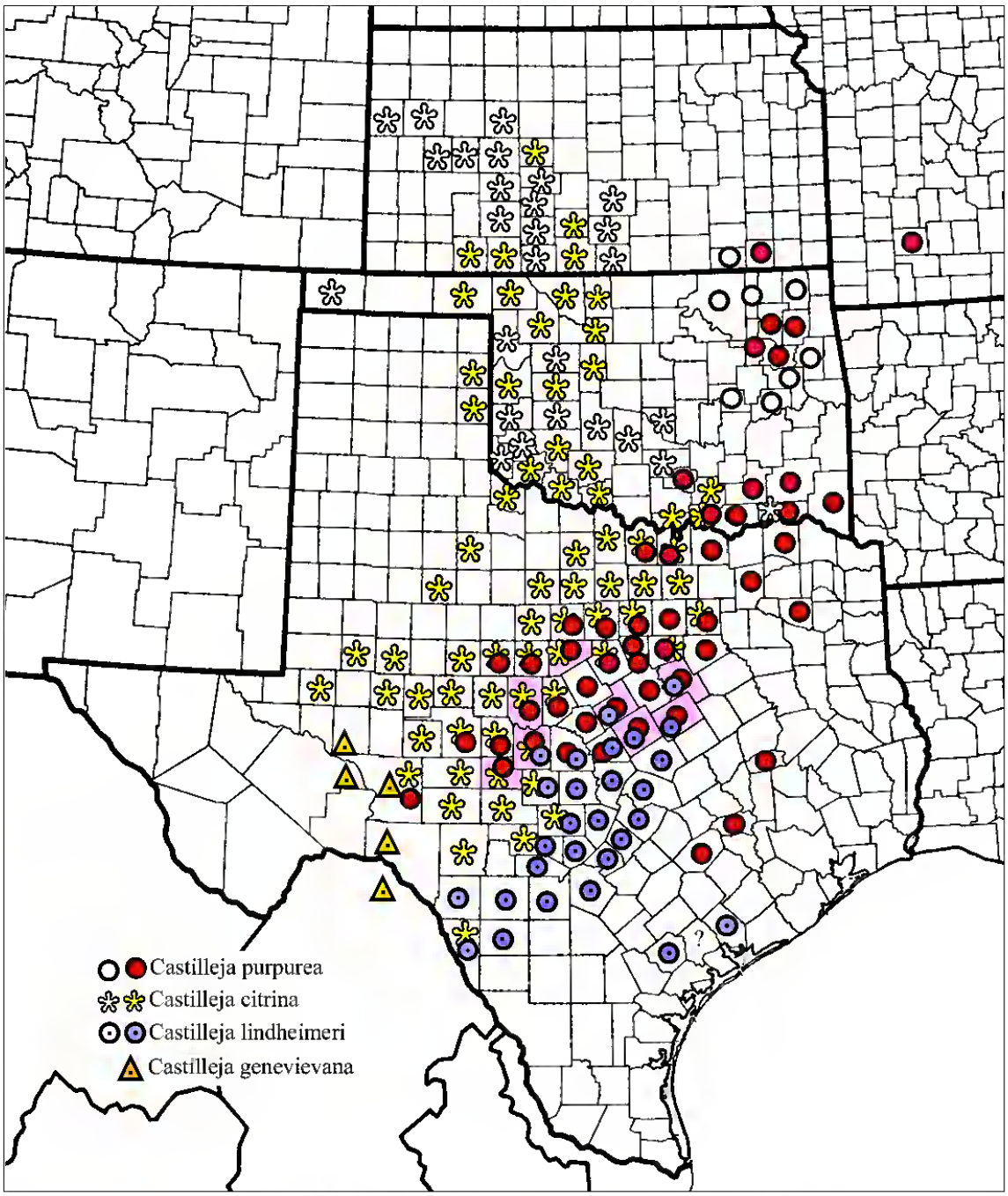

Figure 1. Distribution of the *Castilleja purpurea* complex and the yellow-bracted *C. genevievana*. Counties with pink background are those in which populations widely variable in bract and calyx color are known to occur. Uncolored symbols are from OVPD (2012) and BONAP (2013). Texas county records added from Pennell (1935): *C. lindheimeri* – Jackson; *C. purpurea* – Fayette. The record from Greene Co., Missouri is this: Percy Cave, Apr 1903, *P. C. Standley s.n.* (US, photo MO!).

The morphological consistency (aside from color) and geographic coherence of this complex indicates that these three entities comprise a closely related group, probably arisen from a single ancestor (see potential caveat below regarding *Castilleja citrina*). Rare yellow color variants within *C. purpurea* far-removed from *C. citrina* populations, and color variants within *C. citrina* and *C. lindheimeri*, perhaps reflect an ancestral gene pool. This and the variability of populations at contact zones have formed the rationale for treating them within a single species.

The alternative proposed here, recognition of three separate species, emphasizes their largely consistent morphology, the relatively narrow zones of hybridization along areas of contact, compared to the much larger areas within which each of the three is consistent, and the consistent distinction between *Castilleja citrina* and *C. purpurea* even within a significant area of sympatry. A somewhat analogous situation exists between the widespread *C. miniata* Douglas ex Hook. and the primarily Rocky Mountain species *C. rhexifolia* Rydb. (Holmgren 1984). If broader zones of hybridization and introgression existed among the entities, their recognition as varieties within a single species would seem more appropriate.

The taxonomic interpretation is subjective, depending upon the underlying species concept — no formal definition exists regarding how strictly isolating mechanisms must limit hybridization and/or introgression in order to justify the recognition of distinct species. Subjectivity in the instance at hand may extend further, since evidence in support of one or the other interpretation might be regarded as equivocal. It does seem likely, however, that treating the entities at specific rank will have greater effect in evoking further study.

Hybridization among these taxa and the conspicuousness of populational variability probably greatly increased as road corridors were developed. Pennell himself in 1920, presumably before exceptionally wide rights-of way became characteristic of Texas roadways, made collections of *Castilleja* in Texas (in Bexar, Coleman, Hays, Kendall, Kerr, Randall, Tom Green, and Travis counties, as cited in the 1935 study, mostly in the ranges of *C. citrina* and *C. lindheimeri*), but he did not mention highly variable populations in his 1935 study. In fact, he noted specifically (p. 531) that *C. lindheimeri* "is not so variable in color as Gray supposed."

Hybridization between the *Castilleja purpurea* complex and other species

Interspecific hybridization is common in *Castilleja* (Egger 1994) and taxonomic implications of its occurrence must be interpreted in context. Pertinent to the present situation, hybrids and hybrid swarms between *C. purpurea* and *C. indivisa* Engelm. are observed where they are sympatric. Figure 12 shows such a hybrid at a locality where both species in typical expression were growing (McCulloch Co., *Egger 851*, WTU). At one site in Coryell Co., Texas, intermediates and apparent backcrosses toward both parents produced a wide range of combinations of morphological features, including bract and calyx color, corolla, calyx, and leaf morphology, habit, and even duration (judging from the root development) (*Nesom 7279–7283*, TEX; Nesom 1992). Similar interactions between these two species have been observed at other Texas localities (e.g., Bosque Co., *McBryde 3022*, SMU; Wise Co., *Swadek 156*, BRIT), though in at least some other mixed populations hybrids are rare and likely first generation (e.g., Hill Co., *Egger s.n.*, WTU). In the latter population, two apparent hybrids were collected for chromosomal analysis and proved to have irregularities, including anomalous chromosome numbers of $n = 14$ and $n = 16$ in a genus with a base number of $x = 12$. Hybrids also occur between *C. indivisa* and *C. lindheimeri* (e.g., Hays Co., *Nesom 7283*, TEX) and *C. indivisa* and *C. citrina* (e.g., Clay Co., *Burgard 115*, BAYLU; Travis Co., *Clary s.n.*, BRIT, TEX). *Castilleja indivisa* is probably most closely related to *C. coccinea* (L.) Spreng. of the eastern USA, *C. scorzonerifolia* Kunth widespread in Mexico, and *C. rigida* Eastw. of trans-Pecos Texas and north-central Mexico, and *C. purpurea* and *C. indivisa* would never be considered conspecific, based on their propensity to hybridize.

The putative hybrids between *Castilleja citrina* and *C. indivisa* in Travis Co. (SW side of Austin, 14 Apr 1992, *Clary s.n.*) apparently are sterile, as the ovaries are unexpanded even in the oldest, withered flowers and no seeds are formed. The label notes that there was a "small population of yellow-bracted plants mixed with *C. indivisa*. Intermediates apparently not present." The yellow-bracted plants have lobed leaves and bracts but the bracts are unusually broad and the inflorescence uncharacteristically loose for *C. citrina*.

The geographic ranges of *Castilleja citrina* and *C. genevievana* Nesom (Fig. 8) approach each other in southwest Texas (Fig. 1) but do not become contiguous. The latter is mostly entire-leaved, but with lobed bracts, and probably is closely related to the red-bracted *C. integra* A. Gray, but it would be interesting to know whether these two closely geographically associated yellow-bracted species are independently evolved or whether their yellow display might reflect shared ancestry. If the latter, the case for treating *C. citrina* at specific rank would be strengthened.

Taxonomy of the *Castilleja purpurea* complex

1. Bract and calyx apices yellow, less commonly orangish yellow ..... **Castilleja citrina**
1. Bract and calyx apices mostly shades of red, purple, and pink, rarely yellowish or white.

2. Bract and calyx apices predominantly purple to pinkish purple, varying to red, reddish orange, burnt orange, peach, light yellow, creamy, and rarely white (albino) ..... **Castilleja purpurea**
2. Bract and calyx apices red to reddish orange or orange ..... **Castilleja lindheimeri**

CASTILLEJA CITRINA Pennell, Proc. Acad. Nat. Sci. Philadelphia 73(3C): 532. 1922. *Castilleja purpurea* var. *citrina* (Pennell) Shinners, Spring Fl. Dallas-Ft. Worth, 410. 1958. **TYPE: USA. Texas**. Coleman Co.: Talpa, stony limestone knoll, 20 May 1920, *F.W. Pennell 10516* (holotype: NY!; isotypes: DS!, GH!, K! digital image!, MO! digital image!, OKLA!, PH!, TEX! digital image!, US!).

Castilleja labiata Pennell, Proc. Acad. Nat. Sci. Philad. 73(3C): 530. 1921[1922]. **TYPE: USA. Texas**. Tom Green Co.: San Angelo, stony prairie, uncommon, 19 May 1899 *W.L. Bray 353* (holotype: US! digital image!; isotype: TEX! digital image!).

Bract and calyx apices yellow (sometimes described as chrome yellow or lemon yellow), less commonly orangish yellow. Figures 4, 6, 7.

Flowering (Mar–)Apr–May. Calcareous prairies, sandy fields, gravelly limestone hillsides, limestone outcrops, roadsides, mesquite, juniper, oak-juniper, and post oak woodlands; 300–800 m; Kans., Okl., Tex.

CASTILLEJA PURPUREA (Nutt.) G. Don, Gen. Syst. Gard. Bot. 4: 615. 1838. *Euchroma purpurea* Nutt., Trans. Amer. Philos. Soc., n.s. 5(6[2]):180. 1837[1835]. **TYPE: USA. Oklahoma**. [probably Choctaw Co.]: "On rocks in the hilly prairies of Red river," May 1819, *T. Nuttall s.n.* (holotype: BM! digital image!; isotypes: K-HOOK(2)! digital image!, PH!).

Nuttall collected in present-day eastern Oklahoma in the summer of 1819 (Nuttall 1821; Lawson 2004). In late May through the first half of June, he explored and botanized along the Kiamichi River, mostly in present day Choctaw, Pushmataha, and LeFlore counties, to its mouth at the Red River.

Castilleja purpurea (Nutt.) G. Don f. *corallina* Waterf., Rhodora 56: 160, 1954. **TYPE: USA. Oklahoma**. Choctaw Co.: Prairies on "blackland" (shallow limestone-derived soil), 0.5 mi N of the junction of Hwys 271 and 70, NW of Hugo, 15 Apr 1950, *U.T. Waterfall 9287* (holotype: OKLA!; isotype: GH!).

Castilleja × *williamsii* Pennell [pro species], Acad. Nat. Sci. Philadelphia Monogr. 1: 530. 1935. **TYPE: USA. Texas**. Goliad Co.: Goliad, Apr 1927, *Rev. C.B. Williams 116* (holotype: PH!;

isotype: TEX! digital image!). Pennell cited these as paratypes: Washington Co.: Brenham, *Hobart s.n.* (GH); without locality, *Drummond 286* (GH).

Bract and calyx apices predominantly purple to pinkish purple, varying to red, reddish orange, orange, peach, light yellow, creamy, and rarely white (albino forms). Many other phrases are used to describe the colors, especially in variable populations, e.g., purplish red, rose, scarlet rose, purplish rose, burnt orange, lavender pink, cerise pink. Figures 2, 3.

Flowering (Mar–)Apr–May. Calcareous prairies, rocky fields, rocky limestone roadbanks, hills, and ledges, calcareous and sandy roadsides, sandy hillsides, juniper, juniper-oak, and post oak woodlands, post oak-hackberry thickets; 250–600 m; Kans., Mo., Okl., Tex.

The type of *Castilleja williamsii*, from Washington Co., Texas, has entire leaves but the bracts are trifid, the bracts and calyces are purplish, and the thick, woody roots indicate that it is perennial. *Williams 115* (PH, TEX!), apparently collected from near the type of *C. williamsii* (*Williams 116*, perhaps the same population), has lobed leaves and was cited by Pennell (p. 530) among the "specimens examined" for *C. purpurea*. A more recent collection from Washington County (3 Apr 1990, *Jones 4167*, VDB) is identified here as typical *C. purpurea*. The plants of *Williams 116* perhaps are *C. purpurea* with genetic influence from *C. indivisa* and are appropriately identified as *C.* × *williamsii*.

Entire leaves also occur elsewhere in *Castilleja lindheimeri*, e.g., Travis Co. (*Albers s.n.*, SMU; *Carr 4629*, BRIT; *Jones 4273*, VDB; *McCart 6693*, SMU) – in these, leaves on the proximal 2/3 of the stem are entire while those distal are lobed. Entire leaves in *C. citrina*, similarly mostly proximal cauline, also occur in Kansas, e.g. Clark Co. (*Brooks 14695*, VDB), Meade Co. (*Freeman 10556*, VDB) and probably in Texas and Oklahoma as well.

CASTILLEJA LINDHEIMERI A. Gray, Syn. Fl. N. Amer. 2(1): 298. 1878. *Castilleja purpurea* var. *lindheimeri* (A. Gray) Shinners, Spring Fl. Dallas-Ft. Worth, 410. 1958. **TYPE: USA. Texas.** [Gillespie Co.:] Pierdenales, mountain prairies on somewhat moist places, Apr 1847, *F. Lindheimer 385*, Flora Texana Exsiccata 669 (holotype: GH digital image!; isotypes: MO 4 sheets!). The specimen was annotated by Gray as *Castilleja lindheimeri* and noted by Pennell in 1930 as the "TYPE" and mistakenly by Egger in 1996 as the holotype. Protologue: "Stony or fertile mountain prairies, on the Pierdenales and Guadalupe, W. Texas, Lindheimer, &c."

Castilleja mearnsii Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 530. 1935. **TYPE: USA. Texas.** Kinney Co.: Ft. Clark, 15 Mar 1893, *E.A. Mearns 1291* (holotype: US! digital image!; isotype: PH!).

Bract and calyx apices red to reddish orange or orange. Figures 10, 11.

Flowering Mar–May. Pastures, grassland, calcareous and sandy roadsides, rocky limestone roadbanks, slopes, and ridges, among granite boulders, juniper, oak-juniper, and live oak woodlands; 300–800 m; Tex.

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Figure 2. *Castilleja purpurea* in typical form. Ca. 5 miles east of Santa Anna, along U.S. Hwy 67, Coleman Co., Texas, 20 Apr 1997.

Figure 3. *Castilleja purpurea* in typical form. Ca. 3 miles east of Bangs, Brown Co., Texas, 20 Apr 1997

Figure 4. *Castilleja citrina* in typical form, with immediately adjacent plants of *C. purpurea* perhaps with influence of *C. citrina*. Figure 5 shows another view of the same population. Ca. 3 miles east of Talpa, Coleman Co., Texas, 20 Apr 1990. Talpa is the type locality for *C. citrina*.

Figure 5. Variable population, including forms apparently intermediate between *C. citrina* and *C. purpurea*. Ca. 3 miles east of Talpa, Coleman Co., Texas, 20 Apr 1990. *Castilleja citrina* in typical form occurs at this site (Fig. 4). Coleman County is slightly northwest of the known range of *C. lindheimeri*, but the brick red colored plants suggest that its influence also may be showing here.

Figure 6 *Castilleja citrina* population in typical form. East of Ballinger, Runnels Co., Texas, 6 Apr 1997.

Figure 7. *Castilleja citrina* in typical form. West of Benoit, Runnels Co., Texas, 20 Apr 1997.

Figure 8. *Castilleja genevievana.* East of Sheffield, Crockett Co., Texas, 19 Apr 1997. Does the yellow color indicate shared ancestry with *C. citrina*?

Figure 9. *Castilleja citrina*, orangish yellow, perhaps reflecting influence of *C. lindheimeri* in an area where the two are parapatric or narrowly sympatric. West of Fredricksburg, Gillespie Co., Texas, 3 Apr 1990.

Figure 10. *Castilleja lindheimeri* in typical form. Cypress Creek Park, northwest of Austin, Travis Co., Texas, 3 Apr 1990.

Figure 11. *Castilleja lindheimeri* in typical form. West of Lometa, Lampasas Co., Texas, 20 Apr 1997.

Figure 12. *Castilleja indivisa* x *C. purpurea*, presumed F1 hybrid (right) with typical *C. indivisa* (left), ca. 3 miles east of Brady, McCulloch Co., Texas, 20 Apr 1997. In the hybrid plant, note the deeply divided leaves and relatively longer corolla beaks of *C. purpurea* and the largely emarginate calyces of *C. indivisa*, along with the more or less intermediate coloration of the bracts and calyces. The bracts are red like *C. indivisa*, the purple of *C. purpurea* apparently not expressed even in intermediacy.

Sorrie, B.A. 2014. The maritime variant of *Smilax bona-nox* (Smilaceae). Phytoneuron 2014-16: 1–3. Published 6 January 2014. ISSN 2153 733X

THE MARITIME VARIANT OF *SMILAX BONA-NOX* (SMILACACEAE)

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ABSTRACT

A variety of *Smilax bona-nox* L. described in 1944 lacks a Latin diagnosis and therefore was not validly published. Morphological and habitat characters strongly suggest that the variety is real, and it is recognized here by valid publication: **Smilax bona-nox** L. var. **littoralis** Coker ex Sorrie, **var. nov.**

In his excellent monograph on "The Woody Smilaxes of the United States," William Chambers Coker (1944) described variety *littoralis* Coker within *S. bona-nox* L. His type description stated "Tubers without spines and after a few months lead gray; stolons with few or no spines; aerial canes entirely without scurfy 'hairs.' Otherwise as in the species." Coker designated a type specimen, but without a Latin diagnosis the name was not validly published under the Botanical Code of that time. Here, I validate Coker's epithet and provide additional taxonomic and habitat data.

Smilax bona-nox L. var. **littoralis** Coker ex Sorrie, **var. nov.** TYPE: USA. **South Carolina**. Horry Co.: Myrtle Beach, 2 Jul 1942, *W.C. Coker* & *B.E. Smith s.n.* (holotype: NCU). The label on a syntype is identical but also reads "sandy flats behind dunes" (NCU 3 sheets).

Plants as in typical *Smilax bona-nox* but aerial stems without scurfy hairs, runners with few or no spines, tubers with few and poorly developed spines, and leaf major veins 7–9 (vs. 5–7).

Specimens annotated by Coker as var. *littoralis* are from maritime habitats in South Carolina. He did not annotate specimens from other states as var. *littoralis* because no specimens available to him at NCU bore underground parts and very few possessed lower portions of aerial stems. With such a restricted range, and requiring tubers, runners, and lower stems for identification, it is understandable that subsequent authors have not recognized var. *littoralis*. Ahles (1968) and Godfrey and Wooten (1981) omitted any mention of it; Holmes (2002) listed it in synonymy. Herbarium specimens collected since Coker rarely have lower stems or underground parts present. Nonetheless, Coker in his monograph showed a mastery of the genus and it is just as useful today as then; it is therefore likely that his observations have merit. I here provide supporting and additional data to his description.

Morphological characters

To assess the validity of var. *littoralis*, and to develop key characters on aerial parts, I tested a number of potential morphological characters from specimens at NCU: fruit size, fruit surface, tepal length, tepal shape, tepal color, leaf morphology, and leaf venation. I found that mature fruit size was essentially identical between var. *bona-nox* and var. *littoralis*. Fruits were shallowly to deeply puckered (following pressing and drying) and surfaces varied from dull to shiny in both taxa. Leaf shape and size overlapped completely; leaf margin thickness and spininess showed complete overlap. However, tepals and leaf veins proved to be informative.

Applying certain of these criteria to NCU specimens proved to be informative. Maritime specimens which had lower portions of stems present showed no trace of raised stellate hairs. All

inland specimens with lower portions of stems present showed abundant raised stellate hairs. This character is extremely useful and apparently diagnostic — with living plants, I have used this single character to distinguish with near 100% accuracy maritime plants from inland plants of floodplain swamps. Dried specimens seldom have aerial stems present, however.

Leaf venation proves to be highly useful, despite some overlap. Maritime specimens show 7–9 major veins arising from the summit of the petiole, whereas inland plants show 5–7 major veins.

Specimens from barrier islands and other maritime habitats have short dark tepals, pointed but not attenuate tepals,. In contrast, all inland specimens have long pale tepals with attenuate tips. Tepal shape and color (when dried) are rather subjective characters to evaluate, and so I have omitted them from the revised type description above. Nonetheless, with caution they can be useful.

Other morphological differences. Living plants of var. *littoralis* produce shorter aerial stems than those of var. *bona-nox*. In tall maritime forests of the Outer Banks of North Carolina, var. *littoralis* seldom exceeds 5 meters in height, whereas var. *bona-nox* of inland swamps regularly exceeds 10 meters (pers. obs.). On open dunes var. *littoralis* often scrambles over shrubs but more often forms irregular patches of tangled growth less than a meter high. Plants are subject to continual salty breezes, frequent sand spray, and occasional storm overwash.

Table 1 compares various characters that have taxonomic value.

Table 1. Morphological and habitat characters of *Smilax bona-nox* var. *bona-nox* and var. *littoralis*.

character	var. *bona-nox*	var. *littoralis*
tuber surface	with abundant tiny rounded bumps, plus many sharp to blunt spines	with abundant tiny rounded bumps, with no spines or few and poorly developed sharp to blunt spines
runners ("stolons" per Coker)	with spines on nodes and internodes	"almost without spines" (Coker 1944)
aerial stems	lower portion covered with abundant tiny raised bumps, each with compound stellate hairs distally	lower portion smooth, stellate hairs absent
number of major leaf veins arising from summit of petiole	5–7	7–9
tepal length	4.5–6.0 mm	4.5–5.0 mm
tepal shape	attenuate	pointed, but not attenuate
tepal color (dried specimens)	tan to pale brown	dark brown to pale brown
habitat (from NC and SC specimens)	moist floodplains, alluvial flats, bottomlands, natural levees, river banks, swamp forests, "moist hilltop", "oak-hickory woods", "xeric woodland border." Primarily in deep shade.	maritime dunes, sandy pine woods on barrier islands, maritime shrub thickets, sand flats behind dunes, edges of brackish marshes, maritime forests. Primarily in full sun, but also light shade.

Habitat

Smilax bona-nox var. *littoralis* occurs strictly in plant communities on maritime sands. These include semi-stable sand dunes, shrub thickets, pine and pine-oak woods, maritime forests on oldder dunes, sand flats behind dunes, and edges of brackish marshes. Plants grow primarily in full sun and light shade but also in moderate shade. In contrast, var. *bona-nox* inhabits moist/wet soils of floodplain forests on older substrates, subject to temporary flooding.

Range

Specimens at NCU indicate a range from southeastern Virginia (probable) to south-central Florida and northwestern Florida. States and counties of occurrence are as follows. **Virginia**. Northampton Co.: End of County Road 662 on Ramshorn Bay (E of Eastville), 5 Mar 1966, *James 3755* (NCU; leaves with 9 major veins). **North Carolina**. Brunswick, Carteret, Craven, Currituck, Dare, Hyde, Pamlico, Pender counties. Carteret Co.: near Shackleford [Island] Point, 11 Apr 1898, *Ashe s.n.* (NCU). **South Carolina**. Berkeley, Charleston, Georgetown, Horry counties. **Georgia**. McIntosh Co.: Sapelo Island, climbing small trees in live oak woods near N end of island, 8 Aug 1956, *Duncan 20422* (NCU). **Florida**. Duval, Franklin, Highlands, Levy counties. Franklin Co.: Cape St. George Island, frequent with *S. auriculata* in sandy loam of hammock, bay side of island, 11 Apr 1985, *Anderson 7939* (NCU; leaves with 9 major veins, tepals short, dark, pointed).

Rarity status

Range-wide, *Smilax bona-nox* var. *littoralis* cannot be considered a rare taxon. It is common and characteristic of the Outer Banks and Core Bank of North Carolina and at least locally common in South Carolina. It may well be rare in Virginia, however, and vouchers should be collected with lower stems.

Taxonomic status

While the combination of morphological and habitat data may suggest specific status, I will defer here until additional material has been examined at other herbaria and until genetic work has been conducted. I think it important to verify the leaf venation and tepal characters in conjunction with stem trichomes (on the same specimens) in order to be confident of identification. Many incomplete specimens cannot now be reliably identified because they lack stems.

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Alan Weakley suggested valuable improvements to the manuscript.

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Hrusa, G.F. 2014. *Diplacus bicolor*, correct name in the genus *Diplacus* for *Mimulus whitneyi* (Phrymaceae). Phytoneuron 2014-17: 1. Published 21 January 2014. ISSN 2153 733X

DIPLACUS BICOLOR, CORRECT NAME IN THE GENUS *DIPLACUS* FOR *MIMULUS WHITNEYI* (PHRYMACEAE)

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ABSTRACT

Diplacus bicolor (A. Gray) Hrusa, **comb. nov.**, is the correct name in *Diplacus* for *Mimulus whitneyi* A. Gray, 1886, a nomen novum based on *Eunanus bicolor* A. Gray, 1868.

Review of a draft version of the *Diplacus* treatment for Volume 17 of *Flora of North America North of Mexico* revealed that the listed combination *Diplacus whitneyi* (A. Gray) G.L. Nesom (Phytoneuron 39: 29. 2012), based on *Mimulus whitneyi* A. Gray (Syn. Fl. N. Amer. ed. 2, 2(1): suppl. 445. 1886), has an earlier epithet available.

In the protologue for *Mimulus whitneyi* Asa Gray cited as a synonym the legitimate *Eunanus bicolor* A. Gray, Proc. Am. Acad. 7: 381. 1868. The new epithet '*whitneyi*' was proposed due to the existing name *Mimulus bicolor* Hartw. ex Benth. (Pl. Hartwegianae 328. 1849; = *Erythranthe bicolor* (Hartw. ex Benth.) G.L. Nesom & N.S. Fraga, Phytoneuron 39: 36. 2012). As there is no impediment to use of the epithet '*bicolor*' at specific rank in *Diplacus*, the combination *Diplacus whitneyi* is superfluous (ICN Art. 52.2). The resulting absence of a legitimate name for *Eunanus bicolor* in the genus *Diplacus* is rectified with the following new combination.

DIPLACUS BICOLOR (A. Gray) Hrusa **comb. nov**. *Eunanus bicolor* A. Gray, Proc. Amer. Acad. Arts 7: 381. 1868. *Mimulus nanus* Hook. & Arn. var. *bicolor* (A. Gray) A. Gray in Brewer & S. Wats., Bot. Calif: 1: 564. 1876. *Mimulus whitneyi* A. Gray, Syn. Fl. N. Amer. ed. 2 (1, Suppl.): 445. 1886 [nomen novum in *Mimulus* for *Eunanus bicolor* A. Gray, not *Mimulus bicolor* Hartw. ex Benth., Pl. Hartwegianae 328. 1849]. *Diplacus whitneyi* (A. Gray) G.L. Nesom, Phytoneuron 39: 29. 2012 [nom. illeg.]. **LECTOTYPE** (Grant 1925, p. 307): **USA. California**. Fresno Co.: High Sierras, 1863, *W.H. Brewer 2785* (GH digital image!).

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RECOGNITION OF *ERIOGONUM CALCAREUM* VAR. *SCEPTRUM* (POLYGONACEAE), AN IDAHO ENDEMIC

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ABSTRACT

Ongoing field and herbarium research on *Eriogonum calcareum* (Polygonaceae) of southeastern Oregon and southwestern Idaho has shown that the common phase in Idaho is a distinct expression that is worthy of recognition. Thus, the new combination **Eriogonum calcareum** (S. Stokes) Grady & Reveal var. **sceptrum** (Reveal) Reveal & Mansfield, **comb. nov.**, is proposed based on the 1989 name *E. ochrocephalum* var. *sceptrum*.

When Grady and Reveal (2011: 35) elevated *Eriogonum ochrocephalum* S. Wats. subsp. *calcareum* S. Stokes (1936: 92) to the rank of species, they defined their *E. calcareum* (S. Stokes) Grady & Reveal broadly and did not recognize the phase commonly found in Idaho, namely *E. ochrocephalum* var. *sceptrum* Reveal (1989: 252; 2012: 298). More intense study of *E. calcareum* by Mansfield and his students, however, has shown that the two phases are distinct. To make available the appropriate nomenclature for their publications, and to make the name available for a field guide to *Eriogonum* and relatives for a joint meeting of The Eriogonum Society and The Idaho Native Plant Society to be held in Twin Falls, Idaho, in June 2014, the following combination is proposed.

Eriogonum calcareum (S. Stokes) Grady & Reveal var. **sceptrum** (Reveal) Reveal & Mansfield, **comb. nov.** *Eriogonum ochrocephalum* S. Wats. var. *sceptrum* Reveal, Phytologia 66: 252. 1989. **Type. USA. Idaho.** Owyhee Co.: 11 mi SW of Bruneau, 7 Jul 1974, *J.L. Reveal 3687* (holotype: US; isotypes: ARIZ, ASU, BRY, CIC, COLO, DAV, GH, IDS, GH, NY, RM, RSA, TEX, UTC).

Plants herbs, erect, scapose, 2–4.5(–5) dm tall; **stems** spreading, without persistent leaf bases, up to 1/5 height of plant, the caudex stems slightly matted, the aerial flowering stems erect, slender, solid, not fistulose, 1.5–4.5 dm long, glabrous; **leaves** basal, 1 per node, the petioles 1–3 cm long, tomentose, the blades mostly narrowly elliptic to oblong, (0.6–)1–3.5(–4) cm long, (0.3–)0.5–1 cm wide, densely white-tomentose on both surfaces, the margins plane; **inflorescences** subcapitate, 1.5–2.5 cm long, the subtending bracts 3, scalelike, narrowly triangular, 1–2.5 mm long, often floccose; **peduncles** erect, slender, 0.1–0.5(–0.6) cm long, glabrous; **involucres** solitary on a peduncle, narrowly turbinate to turbinate, 3.5–4.5(–5) mm long, (1.5–)2–3(–4) mm wide, rigid, sparsely floccose to glabrous over the upper half of the tube, the teeth 6–8, erect, 0.5–1 mm long; **flowers** 1–1.5(–2) mm long, usually bright yellow, glabrous, the hypanthium only at base of perianth, the tepals monomorphic, broadly oblong, the stamens exserted, 2.5–3.5 mm long, the filaments pilose proximally; **achenes** light brown, 1.5–2 mm long, glabrous.

Flowering May-Jun. Volcanic ash flats, washes, and slopes with little magnesium, in Chalk Hills and Glenns Ferry formations, in saltbush and sagebrush communities and juniper woodlands; 600–1000 m; Elmore, Owyhee, and Twin Falls cos., Idaho.

Representative specimens. **USA. Idaho.** Elmore Co.: above Rosevear Gulch, S of Glenns Ferry, 13 May 1980, *Grimes et al. 1544* (CAS, CIC, NY); 1 mi W of King Hill, 12 Jun 1989, *DeBolt 1146* (CIC, NY); near Glenns Ferry, 13 Jul 1975, *Reveal 3898* (BRY, CAS, DUKE, F, GH, MICH, MO, NY, OKL, RSA, TEX, UTC). Owyhee Co.: 1.5 mile N of Little Jacks Creek along Vaught Road, 6 Jun 1998, *Atwood 23785* (BRY, MO, NY); W of Grandview, 26 Jun 1989, *DeBolt 1191* (NY); 4 mi W of Oreana, 5 Jul 1980, *Grimes et al. 1759* (BRY, CAS, CIC, NY); 10 mi S of Bruneau, 29 May 1946, *Maguire & Holmgren 26236* (BRY, CAS, CIC, DS, NY, UC, UTC); Hart Creek Canyon, W of Oreana, 8 Aug 1978, *Rosentreter 268* (NY); Little Jacks Creek, "Chalk Hills," Glenns Ferry Formation, 16 Jun 1982, *Smithman et al. LS-0844* (CIC); 12 km NW of Murphy on lacustrine soils, 25 Jun 1991, *DeBolt 1518* (CIC); Sugar Valley Badlands W of Bruneau, 3 Jun 1983, *Rosentreter 3133* (CIC); SE of Oreana, 0.5 mi W of Birch Creek, 11 Jun 2006, *Mansfield 06-37* (CIC). Twin Falls Co.: along Yahoo Creek near Thousand Springs, 8 air mi S of Hagerman, 14 May 1980, *Grimes et al. 1562* (CIC, NY); 10 mi N of Twin Falls, 30 May 1946, *Maguire & Holmgren 26239* (BRY, CAS, CICDS, MO, NY, TEX, UC, UTC); near Banbury Hot Springs, 8 Jun 1979, *Grimes et al. 79-99* (CIC); Tuana Gulch, 31 May 2010, *Smith 8663* (CIC, SRP).

The wand wild buckwheat, *Eriogonum calcareum* var. *sceptrum*, differs from the Harper wild buckwheat, var. *calcareum*, as follows:

1. Involucres sparsely floccose over the distal three-quarters of the tube, sessile or nearly so; scapes (0.7–)1–3 dm long; Oregon (Baker and Malheur cos.), southern Washington (Payette Co.), and Idaho (southern Canyon Co.) ..... var. **calcareum**
1. Involucres glabrous to sparsely floccose over the upper half of the tube, pedunculate; scapes (1.7–)2–4.5(–5) dm long; southwestern Idaho (Elmore, Owyhee, and Twin Falls cos.) ..... var. **sceptrum**

In the field, the var. *sceptrum* is a taller herb with bright yellow flowers that occurs on sites with low magnesium concentrations, unlike var. *calcareum*, which is a shorter plant (0.7–3 dm tall) with (often) pale yellow flowers and common on sites high in magnesium. The two expressions are geographically separate although small, nearby populations of var. *calcareum* in southern Canyon Co. (Idaho) and Payette Co. (Washington) approach populations of var. *sceptrum* in northern Owyhee Co. (Idaho). The most obvious difference is in the inflorescence. In var. *calcareum*, the inflorescence is a tight capitate cluster of numerous, sparsely floccose involucres that are hairy most of their length. In var. *sceptrum* the involucres are subcapitate with the sparsely floccose (and then only near the apex) or glabrous involucres on short peduncles up to 0.6 cm long. Involucres of populations at the northeast end of the range, north of the Snake River, though pedunculate, tend to be more floccose, and, in that respect approach var. *calcareum*.

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THE ECOLOGY AND ABUNDANCE OF *HYMENOXYS TEXANA* (ASTERACEAE)

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ABSTRACT

During 2009-2010, the ecology of *Hymenoxys texana*, Texas Prairie Dawn, was studied at three prairie sites in Harris County, Texas to determine population variations across various saline prairie microhabitats and whether a 1989 recovery plan proposed for the species has been succeeding. Associated plant species, plant community structure and abundance comparisons between years for *H. texana* were also assessed. Densities of *H. texana* varied between zero and 429 individual plants/m^2, with an average of approximately 83 plants/m^2. No overall significant differences in plot densities between sites were found, although a significant increase in *H. texana* occurred across sites from 2009 to 2010. Notable plant associations included *Thurovia triflora, Chloris texensis, Valerianella florifera, Willkommia texana var. texana, Atriplex texana* along with 12 other regionally restricted species for a total of 378 associated taxa. A new Houston Coastal Prairie association is proposed: the *Sporobolus pyramidatus–Spergularia echinosperma–Iva angustifolia–Hymenoxys texana–(Thurovia triflora)* Herbaceous Vegetation, the Houston Saline Prairies association. A checklist of the flora of Warren Ranch and Jack Road Prairies is appended.

Hymenoxys texana (Coult. & Rose) Cockerell (Asteraceae) is an extremely rare (G2S2) endemic plant that is restricted to the Texas Gulf Coastal Plain of Fort Bend, Harris, and Trinity counties. The species is based upon an unnumbered specimen collected in 1889 near Hockley (Harris County), Texas by F. W. Thurow. It was originally described under the name *Actinella texana* by Coulter and Rose (1891). In 1904, Cockerell proposed the new combination *H. texana*. Until 1970, the species appeared to have vanished from Texas botany. It is not listed in Texas Plants – A

Checklist and Ecological Summary by Gould (1962) Correll and Johnston (1970), in the Manual of the Vascular Flora of Texas, stated "Rare in sandy soils near Hockley and Houston, Harris Co., probably extinct (no known collections after 1900)." In 1981, James W. Kessler discovered three populations growing in "buffalo wallows" or small depressions in Harris County, these being the first known collections of this species since 1889-90 (Mahler 1983).

Hymenoxys texana was listed as endangered by U.S. Fish and Wildlife Service (1986). The founding information was assembled by Bridges (1988). Approximately 60 occurrences (TxNDD 2010) of *H. texana* have been recorded, these primarily in Harris County. Unfortunately, many of these occurrences have been lost to development. At the present time, the taxonomy appears to have become stabilized (Bierner 2006) and the number of individuals, distribution, and basic habitat structure is known. The primary objective of this study was to secure information that may be used now (or later) to determine if the recovery plan for *H. texana*, as proposed by Young and Brown (1989) has been succeeding. The study included identifying the habitat for the species, monitoring populations, and documenting associated species, vegetation types (associations), and structure of the community, all with emphasis on demography. Until this report, there have been no demographic studies of the species.

Background

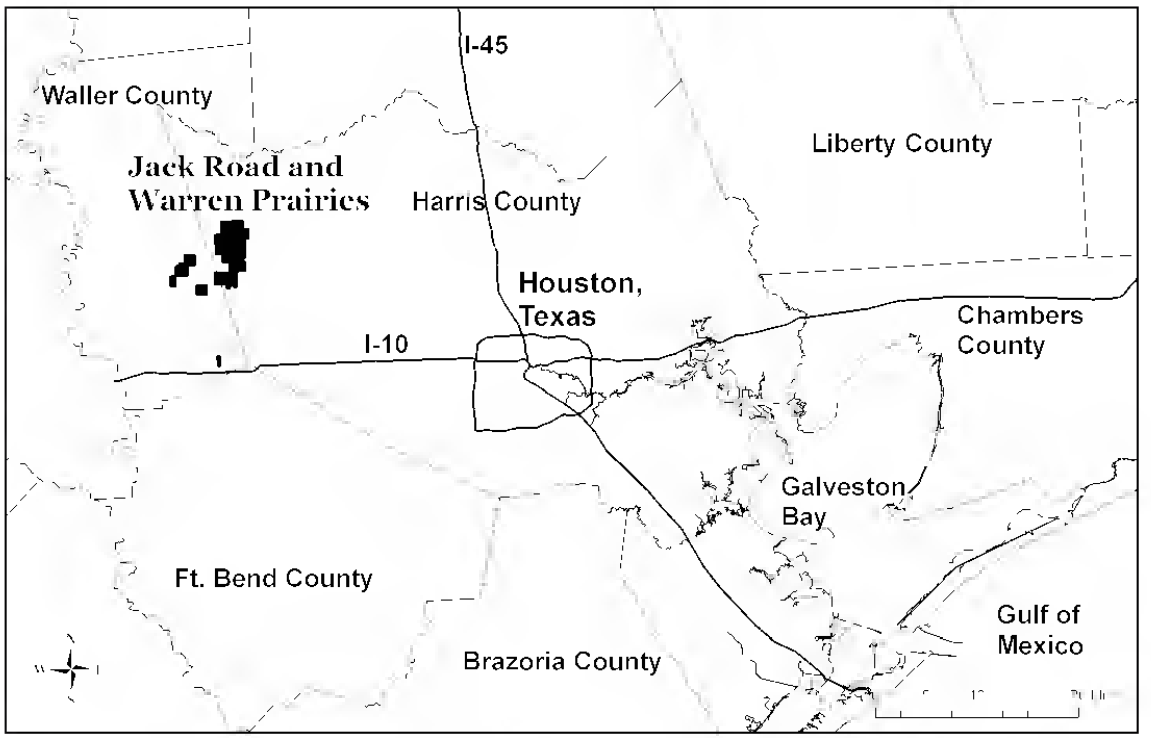
Hymenoxys texana (Fig. 1) is limited to saline prairies with cryptogamic soils within the Houston Coastal Prairie (*Muhlenbergia capillaris* Herbaceous Vegetation Alliance) (National Vegetation Classification System 2012). Many of the species that occur in these saline prairies are absent from or uncommon in adjoining vegetation. These soils are shallow, saline, and support a moderate diversity of annual and perennial herbs that commonly occur in barren slicks and the base of mima mounds (Bierner 2006; Mink et al. 2010). It is thought that the natural pattern of disturbance (droughts, fires, and floods) is necessary to maintain the areas, though the exact role of disturbance is not clear.

Figure 1. *Hymenoxys texana* (Photograph by Singhurst).

Site history

The Katy Prairie region is located in northwest Harris County, Texas, near the city of Katy (Map 1). The area is subject to mixed use, largely involving rotation of crop agriculture (rice), livestock grazing, and, in some areas, salt mining. Katy Prairie Conservancy, a local land trust organized for the preservation of the remaining Katy Prairie remnants, purchased the Warren Ranch property at a 70% buy-in rate. Currently, the remaining 30% remains under the Warren family ownership. Two additional portions of the Warren Prairie, totaling approximately 115 ha (285 acres) were purchased to be preserved as the *Hymenoxys texana* conservation areas. Another portion of the property, the Jack Road Prairie, consisting of 206 ha (511 acres) has a complex system of saline prairies and serves as prime habitat for *H. texana,* but it is in private ownership.

Hymenoxys texana populations have been surveyed in at least one of these three areas in 2003, 2005, 2006, 2008, 2009, and 2010. Before 2008, the surveys were limited to locating *H. texana* populations and inventories of associated plant species. In 2008, a census was conducted to estimate the population size of the Jack Road and Warren Prairie areas. Additionally, the species of each of the three areas mentioned above were enumerated for comparative purposes.



Map 1. Jack Road and Warren Prairies, Katy Prairie Conservancy, Harris and Waller counties, Texas.

Soils

The soil of Jack Road and Warren Prairies — formed from the fluviomarine deposits of the Lissie Formation — is being considered by the Natural Resources Conservation Service (NRCS) as representing its own individual soil series. Currently, the soils on site are predominantly classified as within the Gessner Complex (Gs and Ge) or as Katy Fine Sandy Loam (Kf) (Wheeler, 1976). However, due to the distinctive presence of a natric horizon, the Gessner and Katy Loam series do not accurately reflect the Warren Ranch soil type (NCSS 2012). The natric horizon includes a high

content of exchangeable sodium, an important characteristic and developmental trait of the saline prairie habitat (Pettry & Switzer 1999).

Climate

The area is characterized by a temperate coastal climate. During the growing season of *Hymenoxys texana* (February to April), average ambient temperature ranges from 8.9 C. (48°F) to 26.1 C (79°F). Rainfall averages approximately 22.9 cm (9 inches) for the three month span (National Climatic Data Center 2011).

METHODS

Sampling design and data analysis

Using ArcGIS v9.2, a polygon shape file estimating the location and limits of all saline barrens within the three sections of surveyed property was created. From early February to mid-March, each site was visited to determine the presence or absence of *Hymenoxys texana* in each barren. GPS and Arc Pad 6.0 software were used to find the approximate boundary of each polygon of each population. These were numbered, with a total of 45 randomly selected for inventory. The inventory was conducted by randomly placing a one meter square (1 m^2) quadrat within the boundary of each barren. A census of *H. texana* and inventory of all plant species present were taken.

The abundance data were compared between the three tracts of property and also for the two survey years. The average abundance was calculated and a two-way ANOVA was performed with tract, year, and the possible interaction between them as explanatory variables. Comparisons of means were performed using the Tukey HSD test. All data were square root transformed and assessed to ensure that assumptions of homogeneity of variance and normality of residuals were met (Quinn and Keough, 2002). Tests were carried out in R v 2.10.1 (R Development Core Team 2010).

Floristic inventory

A floristic survey of the prairies was conducted between 2007 and 2010. Voucher specimens were collected and are deposited at Baylor University Herbarium (BAYLU) and the Katy Prairie Conservancy Herbarium (no acronym), Katy Conservancy Field Office, Waller, Texas.

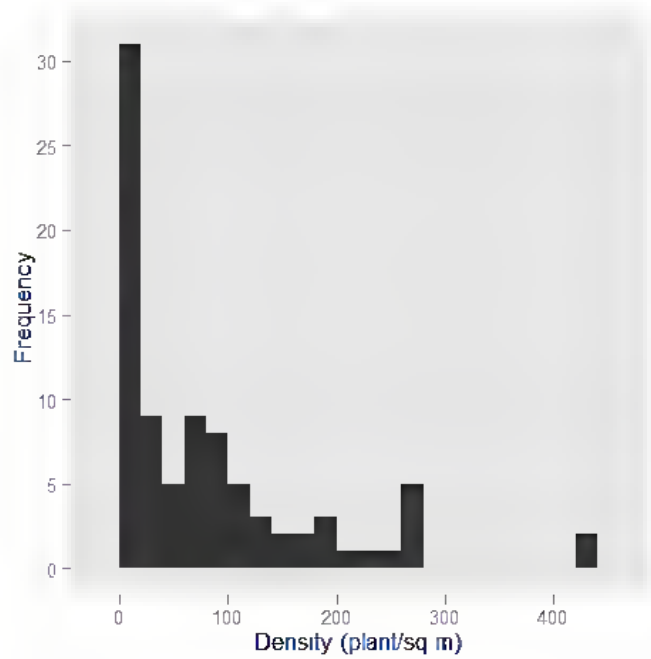


Figure 1 Histogram of *Hymenoxys texana* density per m^2. It is presented here untransformed; for analysis, the data was square-root transformed.

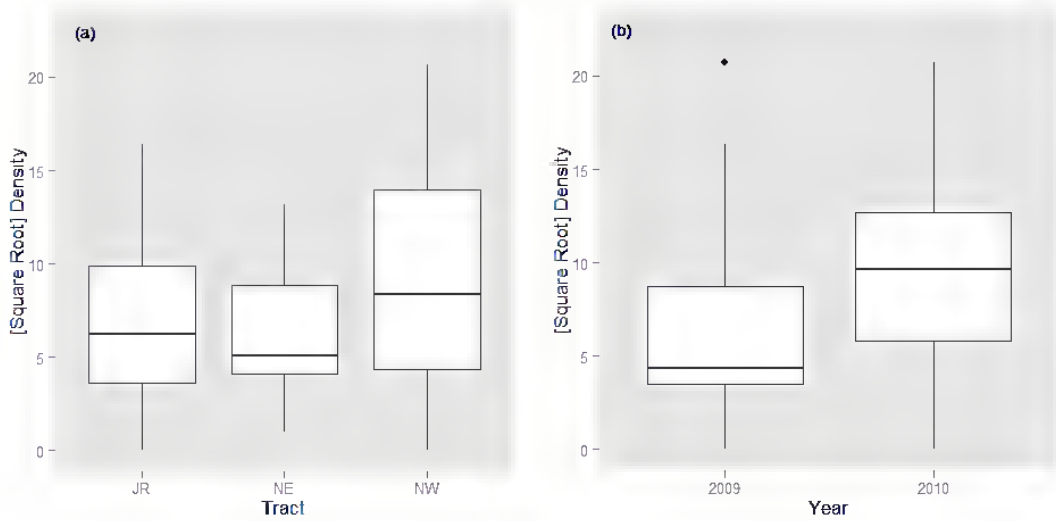


Figure 2. *Hymenoxys texana* mean abundance per m² square-root transformed for normality by (a) tract, and (b) year. The dark middle line in each box represents the median of the data, the lower and upper edges represent the 25% and 75% quartiles, respectively, and the whiskers represent the minimum and maximum values excluding outliers. Maximum-value outliers are considered any data point beyond two times the 75% quartile; thus, one outlier in 2009 was found with a density of 429 plants/m^2. The tracts are as follows: JR is the Jack Rd tract; NE is the Warren Prairie northeast tract; NW is the Warren Prairie northwest tract.

RESULTS

The survey of *Hymenoxys texana* resulted in the discovery of unknown populations in areas previously recorded as lacking the species. Additionally, all previously known occurrences were confirmed to have a continued *H. texana* presence. Within each barren, the three tracts (see Site History) were found to have a variation of density from 0 to 429 individual *H. texana* plants per m² with an average of 83 plants/m² (n = 87) (see Figure 1). No consistent significant differences were found between the densities in the three prairie tracts studied. The ANOVA (Fig. 2) did find that a significant increase in abundance occurred between 2009 and 2010 ($F_{1,81}$ = 9.35, p = 0.003) across all tracts.

Floristic assessment

A total of 378 taxa representing 225 genera and 80 families were documented for the Warren Ranch (Appendix). Of this total 26 (6.9%) are non-native species. Plant families with the largest number of species were Poaceae with 75 (19.8 %), Asteraceae with 58 (15.3%), and Cyperaceae with 28 (7.4%). Several rare and regionally significant plant species were documented and are listed in Table 1. The general distribution and global/state ranks are also presented.

Plant community association

One plant community association within the Houston Coastal Prairie (*Muhlenbergia capillaris* Herbaceous Vegetation Alliance, National Vegetation Classification System 2012) is newly described and restricted to Texas. The *Sporobolus pyramidatus–Spergularia echinosperma–Iva angustifolia–Hymenoxys texana–(Thurovia triflora)* Herbaceous Vegetation (Houston Saline Prairies) is proposed for the first time. This coastal prairie association is restricted to Brazoria, Chambers, Ft. Bend, Galveston, Harris, and Trinity counties in the upper coastal region of Texas. This association has two distinct phases. Phase 1 is dominated by *Sporobolus pyramidatus*, *Spergularia echinosperma*, *Iva angustifolia*, and *Nostoc* (Nostocaceae) (Table 2). Phase 2 is dominated by *Sporobolus pyramidatus*, *Hymenoxys texana*, *Thurovia triflora*, and *Willkommia texana* (Table 2). This association consists of saline prairies primarily dominated by annual plants (54%). The

association persists on sandy and clay prairie landscapes with salty barren spots adjacent to or between mima mounds. The barren spots hold water during the wet season, support *Nostoc* (Nostocaceae) and generally have cryptogamic soils. Characteristic species include *Crassula aquatica*, *Houstonia rosea*, *Iva angustifolia*, *Lepidium densiflora*, *Phemeranthus parviflorus*, *Plantago aristata*, *Spergularia echinosperma*, *Vulpia octoflora*, and *Willkommia texana* var. *texana*. Several rare, endemic and regionally significant plants frequently occur in these barrens. These include *Atriplex texana*, *Chloris texensis*, *Gratiola flava*, *Lechea san-sabeana*, *Schoenolirion wrightii*, and *Valerianella florifera*. Other species of this association include *Ammoselimum butleri*, *Callirhoe involucrata*, *Centunculus minimus*, *Cleomella angustifolia*, *Coreopsis basilis*, *Distichlis spicata*, *Evax verna*, *Evolvulus sericeus*, *Krigia occidentalis*, *Linum imbricatum*, *Nothoscordum bivalve*, *Oenothera spachiana*, *Opuntia macrorhiza*, *Portulaca umbraticola*, *Schoedonardus paniculatus*, *Sida ciliaris*, and *Spartina spartinae*. The plant community association has very few high quality sites remaining and a ranking of G1G2S1S2 (TxNDD 2009) is recommended.

GENUS_SPECIES	COMMON NAME	USA_DISTRIBUTION	RANK
Atriplex texana	Texas saltbush	TX (endemic)	G4S4
Chloris texensis	Texas windmill grass	TX (endemic)	G2S2
Cleomella angustifolia	Northern Rhombo-pod	CO, KS, NE, OK, TX	G5S1S2
Gaura lindheimeri	Lindheimer's butterfly-weed	LA, TX	G3G4S3S4
Gossypianthus lanuginosus var. *tenuiflorus*	woolly cottonflower	AR, LA, OK, & TX	G4S3
Gratiola flava	yellow hedge-hyssop	LA, TX	G3S3
Hymenoxys texana	Texas prairie dawn	TX (endemic & LE)	G2S2 (LE)
Lechea san-sabeana	San Saba pinweed	LA, TX	G4S4
Liatris acidota	slender gayfeather	LA, TX	G4G5S4S5
Lupinus subcarnosus	Texas bluebonnet	AR, TX	G5S5
Phacelia glabra	smooth scorpionweed	AR, LA, OK, TX	G4S2
Rudbeckia texana	Texas coneflower	LA, TX	G3S3
Schoenolirion wrightii	Texas sunnybell	AL, AR, LA, & TX	G3S2
Thelesperma flavodiscum	East Texas greenthread	AR & TX	G3S3
Thurovia triflora	three-flower broomweed	TX (endemic)	G2G3S2S3
Tradescantia subacaulis	stemless spiderwort	AR, TX	G4S4
Valerianella florifera	Texas cornsalad	TX (endemic)	G3S3
Willkommia texana var. *texana*	Texas willkommia	TX (endemic)	G3G4T3S3S4

Table 1 Rare and regionally significant plants inventoried (2003-2010).

SITE	GENUS_SPECIES	% COVER
Jack Road	*Sporobolus pyramidatus*	8.4
	Spergularia echinosperma	6.8
	Iva angustifolia	3.6
	Nostoc spp.	3.3
	Bare	50.8
North Warren Ranch	*Sporobolus pyramidatus*	6
	Hymenoxys texana	3.3
	Thurovia triflora	2.9
	Willkommia texana	2.3
	Bare	55.6

Table 2 Percent cover of flora sampled within KPC Saline Barrens.

DISCUSSION

The overall goal of the research was to collect data for later comparisons, e.g. baseline data. While some data has been collected during earlier studies, these were not in-depth nor in a form serviceable for direct quantitative comparisons. Nonetheless, with the data available [this report and the 2008 study cited above and data from three study sites (see site history above)], it is possible to provide some preliminary assessments. These, however, are not to be considered definitive at this time and very well may be only temporal. This survey found that the number of individuals of *Hymenoxys texana* increased and the number of populations has also increased. The reasons for these increases are not known, but seem to be a result of very favorable climatic conditions during the inventory years and changes in land use. The climate during the past several years was warmer and wetter, the effects of which, while understandable, are not yet understood for *H. texana*. Land use changes included cessation of both planting of row crops and livestock grazing, the major effect being removal of major disturbance.

Another major result of the study is the description of the Houston Saline Prairie Association. *Hymenoxys texana* is limited to two phases of this association. Unfortunately, few high quality sites of Phase 2 are extant. Interestingly, the area also supports 18 plant species that are considered rare or regionally significant (Table 1). Undoubtedly, efforts directed toward the preservation of *H. texana* should benefit these.

Finally, a checklist of the flora of Warren Ranch and Jack Road prairies (Appendix) is completed. Prior to this, only the Katy Prairie proper had a checklist. These accounts are important for documenting later changes in the vegetation composition.

Apparently, *Hymenoxys texana* is sensitive to land use practices, climate (especially rainfall and temperature, during the growing season and possibly at other times), and other factors such as salinity, microclimate, seasonal precipitation variation, etc. The exact nature of the response of the species to these conditions awaits further investigation. Thus, this report serves mainly as an invitation to gather additional data over the next several years. An important facilitation would be to compare populations of the *H. texana* outside of the Houston Coastal Prairies in Trinity County (Poole et al. 2007). This would permit comparisons between the disjunct areas.

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Appendix I. Checklist of the flora of Warren Ranch and Jack Road Prairies

The annotated checklist is divided into pteridophytes, gymnosperms, and flowering plants, which are subdivided into monocots and dicots. Family, genus, and species are arranged alphabetically beneath each major heading. Nomenclature follows Jones et al. (1997), Turner et al. (2003), and United States Department of Agriculture, Natural Resource Conservation Service (2011). Collectors and collection numbers are given as follows: AT = Anita Tiller, JS = Jason Singhurst, KC = Katie Cook, LB = Larry Brown, NS = Nancy Shackelford, and WN = Wesley Neman. An asterisk (*) denotes an introduced species. Vouchers verified at BAYLU and KPCH Herbarium.

PTERIDOPHYTA (FERNS AND FERN ALLIES)

Aspleniaceae

Asplenium platyneuron (L.) B.S.P.

Lygodiaceae

Lygodium japonicum (Thunb.) Sw., JS, NS, & WN 17336*

OPHIOGLOSSACEAE
Ophioglossum crotalophoroides Walt., JS, NS, & WN 17320

POLYPODIACEAE
Pleopeltis polypodioides (L.) Andrews & Windham

CONIFERS

CUPRESSACEAE
Juniperus virginiana L., KC 154

PINACEAE
Pinus taeda L., JS, NS, WN, & AT 17916

MONOCOTS

AGAVACEAE
Yucca louisianensis Trel., JS, NS, WN, & AT 17926

ALISMATACEAE
Sagittaria lancifolia L., KC 143

AMARYLLIDACEAE
Hypoxis hirsuta (L.) Coville, JS, NS, & WN 17339

ARACEAE
Peltandra virginica (L.) Schott, JS 18360

COMMELINACEAE
Commelina erecta L., KC 22
Tradescantia hirsutiflora Bush, JS, NS, WN, & AT 17942
Tradescantia occidentalis (Britt.) Smyth, KC 48
Tradescantia subacaulis Bush, JS, NS, WN, & AT 17978

CYPERACEAE
Carex festucacea Schkuhr ex Willd., JS, NS, WN, & AT 17954
Carex meadii Dewey, JS, NS, & WN 17354
Carex microdonta Torr. & Hook., JS, NS, WN, & AT 17394
Carex triangularis Boeckeler, JS 18258
Cyperus articulatus L., KC 88
Cyperus entrerianus Boeckl, JS, NS, WN, & AT 17973*
Cyperus tria L., KC 128
Cyperus polystachyos Rottb., KC 92
Cyperus pseudovegetus Steud., JS, NS, WN, & AT 17371, JS & WN 17891
Cyperus squarrosus L., JS, NS, WN, & AT 17855; 17980
Cyperus strigosus L., JS, NS, WN, & AT 17979
Cyperus sp., JS 18361
Eleocharis microcarpa Torr., JS, NS, WN, & AT 17340; JS 18247
Eleocharis montana (Kunth) Roem. & Schult., JS, NS, WN, & AT 17983
Eleocharis obtusa (Willd.) Schult., KC 153, JS, NS, WN, & AT 17370
Eleocharis sp., JS, NS, WN, & AT 17984
Fimbristylis caroliniana (Lam.) Fernald, KC 109
Fimbristylis puberula (Michx.) Vahl, KC 109

Kyllinga odorata Vahl, JS 18378
Isolepis carinata Hook & Arn. ex Torr., JS, NS, WN, & AT 17348
Rhynchospora colorata (L.) H. Pfeiffer, KC 123
Rhynchospora corniculata (Lam.) Gray, KC 169, JS 18365
Rhynchospora glomerata (L.) Vahl, KC 109
Rhynchospora rariflora (Michx.) Ell., JS & WN 17988
Rhynchospora recognita (Gale) Kral, JS & WN 17905
Scleria georgiana Core, JS, NS, WN, & AT 17966
Scleria pauciflora Muhl. ex Willd. var. *pauciflora*, JS, NS, WN, & AT 17937
Scleria triglomerata Michx., JS, NS, WN, & AT 17974

IRIDACEAE
Herbertia lahue (Molina) Goldblatt, LB s.n.
Sisyrinchium angustifolium Mill., KC 39, JS 18251
Sisyrinchium atlanticum Bickn., JS, NS, WN, & AT 17928
Sisyrinchium campestre Bickn., JS, NS, WN, & AT 17351
Sisyrinchium mmus Engelm. & Gray, JS, NS, WN, & AT 17350
Sisyrinchium rosulatum Bickn., KC 69, JS, NS, WN, & AT 17380, JS 18492

JUNCACEAE
Juncus brachycarpus Engelm., KC 54
Juncus bufonius L., JS, NS, WN, & AT 17399, JS 18246
Juncus diffusissimus Buckley, KC s.n., JS, NS, WN, & AT 17358
Juncus capitatus Weigel, JS, NS, WN, & AT 17981*
Juncus coriaceus Mack., JS, NS, WN, & AT 17323
Juncus effusus L., JS, NS, WN, & AT 17383; JS 18245
Juncus marginatus Rostk., KC 8, 5, 98
Juncus roemerianus Scheele, JS, NS, WN, & AT 17955
Juncus validus Coville var. validus, KC 99

LEMNACEAE
Lemna minor L.

LILIACEAE
Allium drummondii Regel, LB s.n.
Cooperia drummondii Herbert, KC 107, JS 18399
Cooperia pedunculata Herbert, KC s.n.
Cooperia traubii Hayward, KC 001
Nothoscordum bivalve (L.) Britt., JS, NS, & WN 17319
Schoenolirion wrightii Sherman, LB s.n., JS 18257, JS 18488

MARANTACEAE
Thalia dealbata Fraser ex Roscoe, JS, NS, WN, & AT 17941, JS 18363

ORCHIDACEAE
Spiranthes cernua (L.) Rich., JS & WN
Spiranthes vernalis Engelm. & Gray, KC 10

POACEAE
Agrostis elliottiana Schult., LB s.n.
Agrostis hyemalis (Walt.) B.S.P., JS & NS 17908
Aira elegans Willd. ex Kunth, JS, NS, WN, & AT 17939
Alopecurus carolinianus Walt., KC s.n.& LB, JS 18493
Andropogon glomeratus (Walt.) B.S.P., JS & WN 17890
Andropogon virginicus L. var. *virginicus*, JS & WN 17991
Aristida lanosa Muhl. ex Ell., JS & WN 17860
Aristida oligantha Michx., JS & WN 17869, JS 18373
Aristida purpurascens Poir., JS & WN 17889
Axonopus fissifolius (Raddi) Kuhlm., KC 73, JS & WS 17859
Bothriochloa laguroides (DC.) Herter, KC 44, JS & WN 17861
Bothriochloa longipaniculata (Gould) Allred & Gould, KC 93
Bouteloua curtipendula (Michx.) Torr., WN s.n.
Bouteloua rigidiseta (Steud.) Hitchc., JS & WN 17873
Briza minor L. , JS, NS, & WN 17357*
Bromus catharticus Vahl, JS, NS, WN, & AT 17326 & 17369*
Cenchrus spinifex Cav., KC s.n.
Chasmanthium latifolium (Michx.) Yates, JS & WN 17997
Chloris ×*subdolichostachya* Müll. Berol. (pro sp.) [*cucullata* × *verticillata*], KC 64, 135, JS & WN 17878 *
Chloris texensis Nash, JS & WN 17858
Chloris verticillata Nutt., JS & WN 17857
Cynodon dactylon (L.) Pers., KC 116, JS, NS, WN, & AT 17332*
Dichanthelium aciculare (Desv. ex Poir.) Gould & Clark subsp. *aciculare*, JS & WN 17994
Dichanthelium acuminatum (Sw.) Gould & Clark, JS, NS, WN, & AT 17932
Dichanthelium consanguineum (Kunth) Gould & Clark, KC s.n.
Dichanthelium dichotomum (L.) Gould, JS, NS, & WN 17313, JS 18366
Dichanthelium linearifolium (Scribn. ex Nash) Gould, JS, NS, WN, & AT 17927
Dichanthelium oligosanthes (Schult.) Gould subsp. *scribnerianum* (Nash) Freckmann & Lelong, JS, NS, WN, & AT 17938
Dichanthelium scoparium (Lam.) Gould, KC 71
Dichanthelium sphaerocarpon (Ell.) Gould, KC 58, JS 18374
Dichanthelium villosissimum (Nash) Freckmann var. *villosissimum*, KC s.n., JS 18249
Distichlis spicata (L.) Greene, JS & WN 17877
Elymus virginicus L., JS & WN 17999
Eragrostis intermedia Hitchc., KC s.n.
Eragrostis secundiflora Presl subsp. *oxylepis* (Torr.) S.D. Koch., KC 48,87,100,108, JS & WN 17862, JS 18384
Eliomurus tripsacoides Humb. & Bonpl. ex Willd., JS & WN 17864
Hordeum pusillum Nutt., WN s.n
Leersia hexandra Sw. KC 114
Leptochloa fusca (L.) Kunth ssp. *fascicularis* (Lam.) N. Snow, KC 134
Limnodea arkansana (Nutt.) L.H. Dewey, JS 18372
Lolium perenne L., JS 18250
Muhlenbergia capillaris (Lam.) Trin., JS, NS, WN, & AT 17397, JS & WN 17898
Panicum hemitomon Schult., KC 142, JS 18385
Panicum virgatum L., KC 138
Parapholis incurva (L.) C.E. Hubbard, WN s.n.
Paspalum floridanum Michx., KC 117,137
Paspalum langei (Fourn.) Nash, KC s.n.

Paspalum monostachyum Vasey, JS & WN 17876
Paspalum notatum Flueggé, KC 18,46 *
Paspalum plicatulum Michx., KC 86, JS & WN 17870
Paspalum pubiflorum Rupr. ex Fourn., KC 146
Paspalum setaceum, KC 15,152
Paspalum urvillei Steud., KC 56*
Paspalum sp., JS 18368
Phalaris caroliniana Walt., LB s.n.; JS 18242
Piptochaetium avenaceum (L.) Parodi, JS & NS 17906
Poa annua L., JS, NS, WN, & AT 17329
Polypogon monspeliensis (L.) Desf., JS & WN 17985*
Schedonnardus paniculatus (Nutt.) Trel., LB s.n., JS & WN 17879, JS & NS 17910
Schizachyrium scoparium (Michx.) Nash, WN s.n., JS & WN 17872
Setaria parviflora (Poir.) Kerguelen, KC 90,139, JS & WN 17866, JS 18371
Setaria pumila (Poir.) Roem. & Schult. ssp. *pumila*, KC s.n.*
Sorghastrum nutans (L.) Nash, WN s.n.
Spartina spartinae (Trin.) Merr. ex Hitchc., KC 131, JS 18386
Sphenopholis intermedia (Rydb.) Rydb., JS, NS, WN, & AT 17378
Sporobolus clandestinus (Biehler) Hitchc., WN s.n.
Sporobolus indicus (L.) R. Br., KC 70, JS & WN 17865
Sporobolus pyramidatus (Lam.) Hitchc., KC 104, JS, NS, & WN 17324
Steinchisma hians (Ell.) Nash, WN s.n., JS & WN 17863, JS 18397
Stenotaphrum secundatum (Walt.) Kuntze, JS, NS, WN, & AT 17918*
Tridens strictus (Nutt.) Nash, JS & WN 17995
Urochloa platyphylla (Munro ex C. Wright) R.D. Webster, KC s.n.
Vulpia octoflora (Walt.) Rydb. var. *octoflora*, JS, NS, WN, & AT 17923; JS 18244
Willkommia texana var. *texana* Hitchc., JS, NS, WN, & AT 17388, JS & WN 17875, JS & NS 17908

SMILACACEAE
Smilax bona-nox L., JS, NS, WN, & AT 17398

TYPHACEAE
Typha domingensis Pers., JS & WN 18001

DICOTS

ACANTHACEAE
Ruellia humilis Nutt., KC 91, JS 18410

AMARANTHACEAE
Gossypianthus lanuginosus (Poir.) Moq. var. *tenuiflorus* (Hook.) Mears ex Henrickson, KC 159, JS 18394

APIACEAE
Ammoselinum butleri (Engelm. ex S. Watson) Coult. & Rose, LB & JS, NS, WN, & AT 17300
Daucus pusillus Michx., LB s.n.
Eryngium hookeri Walp., KC 96
Sanicula canadensis L., JS, NS, WN, & AT 17931
Limnosciadium pinnatum (Engelm. & Gray) Math. & Const., JS, NS, WN, & AT 17959
Limnosciadium pumilum (Engelm. & Gray) Mathias & Constance, JS, NS, WN, & AT 17969
Trepocarpus aethusae Nutt. ex DC., JS, NS, WN, & AT 17977

AQUIFOLIACEAE
Ilex decidua Walt., KC 147,158, JS, NS, & WN 17337
Ilex vomitoria Walt., KC 146

ASCLEPIADACEAE
Asclepias oenotheroides Cham. & Schltdl., KC 130
Asclepias viridis Walt., KC 41 & LB, JS & WN 17907
Matelea cynanchoides (Engelm.) Woodson, LB s.n.

ASTERACEAE
Ambrosia psilostachya DC., WN s.n., JS & WN 17903
Aphanostephus skirrhobasis (DC.) Trel., JS, NS, WN, & AT 17934
Arnoglossum ovatum (Walt.) H. Rob., KC 30
Arnoglossum plantagineum Raf., JS 18382
Baccharis halimifolia L., JS & WN 17990
Bigelowia nuttallii L.C. Anderson, JS & WN 17996
Boltonia diffusa Ell., JS & WN 17882, JS 18414
Calyptocarpus vialis Less., JS, NS, WN, & AT 17366
Chaetopappa asteroides Nutt. ex DC., JS, NS, WN, & AT 17958
Chrysopsis pilosa Nutt., KC 120, JS 18418
Cirsium horridulum Michx., JS, NS, WN, & AT 17375
Conoclinium coelestinum (L.) DC., JS & WN 17887, JS 18403
Conyza bonariensis (L.) Cronq., KC 129, JS & WN 17883
Coreopsis basilis (Dietr.) Blake., KC s.n.
Coreopsis tinctoria Nutt., KC 7, 120
Eclipta prostrata (L.) L., JS 18404
Elephantopus carolinianus Raeusch., JS, NS, WN, & AT 17914
Erigeron tenuis Torr. & Gray, JS, NS, WN, & AT 17956, JS 18489
Eupatorium compositifolium Walt., KC 129, JS & WN 17887
Eupatorium rotundifolium L., JS & WN 18000
Eupatorium serotimum Michx., JS 18415
Euthamia caroliniana (L.) Greene ex Porter & Britt., WN s.n., JS & WN 17900
Euthamia gymnospermoides Greene, WN s.n., JS & WN 17899, JS 18380
Evax candida (Torr. & Gray) A. Gray, JS, NS, WN, & AT 17386
Evax verna Raf., JS, NS, & WN 17322; JS 18248
Facelis retusa (Lam.) Sch. Bip., JS, NS, WN, & AT 17328
Gaillardia pulchella Foug., JS, NS, WN, & AT 17945
Gamochaeta pensylvanica (Willd.) Cabrera, KC 74; JS 18241
Gutierrezia texana (DC.) Torr. & A. Gray, WN s.n.
Gymnostyles anthemifolia Juss., JS, NS, & WN 17340*
Helenium amarum (Raf.) H. Rock, KC 11,76, JS & WN 17885, JS 18407
Helianthus angustifolius L., JS & WN 17884, JS 18416
Heterotheca subaxillaris (Lam.) Britt. & Rusby, JS, NS, & WN 17355, JS & WN 17895
Hymenoxys texana (Coult. & Rose) Cockerell, JS, NS, & WN 17305
Hymenopappus artemisiifolius DC., LB s.n.
Hypochaeris microcephala (Sch. Bip.) Cabrera, JS, NS, WN, & AT 17387, JS 18491*
Iva angustifolia Nutt. ex DC., JS & WN 17904
Krigia dandelion (L.) Nutt., JS, NS, WN, & AT 17331
Krigia occidentalis Nutt., JS, NS, & WN 17304
Liatris acidota Engelm. & Gray, KC 75, JS & WN 17897, JS 18409
Marshallia caespitosa Nutt. ex DC., LB s.n.

Packera glabella (Poir.) C. Jeffrey, JS, NS, WN, & AT 17924
Palafoxia rosea (Bush) Cory, JS & WN 17868, JS 18401
Pyrrhopappus carolinianus (Walt.) DC., KC 13
Rudbeckia hirta L., KC 121, JS & WN 17856, JS 18400
Rudbeckia texana (Perdue) P. Cox & Urbatsch, JS & WN 17998, JS 18405
Senecio ampullaceus Hook., JS, NS, WN, & AT 17930
Soliva sessilis Ruiz & Pav., JS, NS, WN, & AT 17309*
Solidago odora Ait., JS & WN 17989
Solidago sempervirens L., JS & WN 17902
Sonchus asper (L.) Hill, JS 18256
Symphyotrichum ericoides (L.) G.L. Nesom, JS & WN 17881
Symphyotrichum patens (Aiton) G.L. Nesom, JS & WN 17993
Thelesperma flavodiscum (Shinners) B.L. Turner, LB s.n.
Thurovia triflora Rose, KC 8, JS & WN 17880, JS 18392
Vernonia baldwinii Torr., JS 18364
Verbesina virginica L., JS & WN 17986
Xanthium strumarum L., JS & WN 17801

BORAGINACEAE
Heliotropium curassavicum L., KC 173, JS, NS, WN, & AT 17400, JS 18377
Heliotropium procumbens Mill., KC 172
Myosotis macrosperma Engelm., JS, NS, & WN 17356

BRASSICACEAE
Cardamine pensylvanica Muhl. ex Willd., JS 18482
Coronopus didymus (L.) Sm., JS 18483*
Lepidium densiflorum Schrad., KC 34, JS, NS, & WN 17316
Lepidium virginicum L., JS, NS, WN, & AT 17347

CACTACEAE
Opuntia humifusa (Raf.) Raf., JS, NS, WN, & AT 17971, JS 18379

CALLITRICHACEAE
Callitriche heterophylla Pursh, JS, NS, WN, & AT 17349 & JS, NS, & WN 17341
Callitriche peploides Nutt., JS, NS, WN, & AT 17975

CAMPANULACEAE
Lobelia puberula Michx., JS & WN 17888
Triodanis biflora (Ruiz & Pav.) Greene, WN s.n.
Triodanis perfoliata (L.) Nieuw., LB s.n.

CAPRIFOLIACEAE
Lonicera japonica Thunb., KC 42

CAPPARACEAE
Cleomella angustifolia Torr., LB s.n., JS 18383

CARYOPHYLLACEAE
Cerastium glomeratum Thuill., JS, NS, WN, & AT 17308
Lepuropetalon spathulatum Ell., JS, NS, & WN 17318
Minuartia drummondii (Shinners) McNeill, JS, NS, WN, & AT 17968; 18260

Sagina decumbens (Ell.) Torr. & A. Gray, JS, NS, WN, & AT 17970, JS 18259
Silene antirrhina L., LB s.n.
Silene gallica L., LB s.n., JS 18263*
Spergularia echinosperma (Celak.) Asch. & Graebn., JS, NS, WN, & AT 17377
Stellaria media (L.) Vill., JS, NS, WN, & AT 17307*

CHENOPODIACEAE
Atriplex cristata Humb. & Bonpl. ex Willd., JS, NS, WN, & AT 17960
Atriplex texana S. Watson, KC 101, JS, NS, WN, & AT 17393, JS 18390

CISTACEAE
Lechea mucronata Raf., JS, NS, WN, & AT 17957
Lechea san-sabeana (Buckley) Hodgdon, JS, NS, WN, & AT 17944

CLUSIACEAE
Hypericum drummondii (Grev. & Hook.) Torr. & Gray, KC 105, JS 18395
Hypericum hypericoides (L.) Crantz, JS, NS, WN, & AT 17951

CONVOLVULACEAE
Dichondra carolinensis Michx., WN s.n.

CONVOLVULACEAE
Evolvulus sericeus Sw., KC 65, JS, NS, & WN 17346
Ipomoea cordatotriloba Dennst., KC s.n., JS & WN 17874

CRASSULACEAE
Crassula aquatica (L.) Schoenl., LB s.n., JS, NS, & WN 17335, JS 18264

DROSERACEAE
Drosera brevifolia Pursh, JS, NS, WN, & AT 17962

EBENACEAE
Diospyros virginiana L., KC 155

EUPHORBIACEAE
Chamaesyce maculata (L.) Small, KC 171
Chamaesyce sp., JS 18408
Cnidoscolus texanus (Müll. Arg.) Small, KC 83
Croton argyranthemus Michx., LB s.n.
Croton capitatus Michx. var. *lindheimeri* (Engelm. & Gray) Müll. Arg., KC 115, JS 18419
Croton glandulosus L., JS 18412
Croton michauxii G.L. Webster, JS & WN 17992
Euphorbia spathulata Lam., JS, NS, & WN 17315 & JS, NS, WN, & AT 17359
Stillingia sylvatica L., JS, NS, WN, & AT 17384
Triadica sebifera (L.) Small, KC 162*

FABACEAE
Baptisia bracteata Muhl. ex Ell. var. *leucophaea* (Nutt.) Kartesz & Gandhi, JS, NS, WN, & AT 17947
Baptisia sphaerocarpa Nutt., JS18484
Chamaecrista fasciculata (Michx.) Greene, KC 29, JS 18396
Desmanthus illinoensis (Michx.) McM. ex Robins. & Fern., KC 94

Galactia sp., JS 18387
Lupinus subcarnosus Hook., JS, NS, WN, & AT 17396
Medicago polymorpha L., JS, NS, WN, & AT 17330*
Mimosa strigillosa Torr. & A. Gray, KC 168, JS 18393
Neptunia lutea (Leavenworth) Benth., JS, NS, WN, & AT 17936
Neptunia pubescens Benth., KC 20
Prosopis glandulosa Torr., JS, NS, WN, & AT 17921
Sesbania drummondii (Rydb.) Cory, JS 18411
Sesbania herbacea (Mill.) McVaugh, JS & WN 17896, JS 18417
Sesbania vesicaria (Jacq.) Elliot , JS 18398
Vicia ludoviciana, JS, NS, WN, & AT 17311

FAGACEAE
Quercus nigra L., JS, NS, WN, & AT 17374
Quercus phellos L., JS, NS, WN, & AT 17950
Quercus margarettae (Ashe) Small, JS, NS, WN, & AT 17948
Quercus stellata Wangenh., JS 18487
Quercus virginiana P. Mill., JS, NS, WN, & AT 17312

GENTIANACEAE
Sabatia campestris Nutt., KC 38, 45, 89, JS, NS, WN, & AT 17382

GERANIACEAE
Geranium carolinianum L., JS, NS, WN, & AT 17952, JS 18262

HYDROPHYLLACEAE
Hydrolea ovata Choisy., KC 160
Phacelia glabra Nutt., LB s.n., JS, NS, WN, & AT 17362

LAMIACEAE
Hedeoma hispida Pursh, JS, NS, WN, & AT 17379
Mecardonia acuminata (Walt.) Small, JS, NS, WN, & AT 17363, LB s.n.
Monarda punctata L., KC 21
Physostegia pulchella C. L. Lundell, JS, NS, WN, & AT 17952
Salvia lyrata L., JS, NS, WN, & AT 17919
Scutellaria parvula Michx., JS, NS, WN, & AT 17961

LINACEAE
Linum imbricatum (Raf.) Shinners, KC 103, JS, NS, WN, & AT 17331, JS 18485
Linum medium (Planch.) Britt. var. *texanum* (Planch.) Fernald, KC 72
Linum striatum Walt., JS, NS, WN, & AT 17935

LYTHRACEAE
Lythrum alatum Pursh , KC 74, 133, JS 18362

MALVACEAE
Callirhoe involucrata, JS, NS, WN, & AT 17344
Sida ciliaris L., KC 19,119
Sida rhombifolia L., JS & WN 17901
Sida spinosa L., JS 18381

MELASTOMACEAE
Rhexia mariana L., KC 156, JS 18370

MENISPERMACEAE
Cocculus carolinus (L.) DC., JS, NS, WN, & AT 17964

MOLLUGINACEAE
Mollugo verticillata L., WN s.n.

MYRICACEAE
Morella cerifera (L.) Small, JS, NS, & WN 17314, JS & WN 17871

OLEACEAE
Ligustrum sinense Lour., JS, NS, WN, & AT 17943*
Fraxinus pennsylvanica Marsh., JS, NS, WN, & AT 17946; JS 18253, JS 18402

ONAGRACEAE
Gaura lindheimeri Engelm. & A. Gray, KC 47, 123, 124
Gaura longiflora Spach, KC 151 & LB s.n.; JS 18265
Gaura mollis James, JS 18389
Gaura sp., JS 18413
Ludwigia linearis Walter, KC 67
Ludwigia octovalvis (Jacq.) P.H. Raven, KC 140
Ludwigia peploides (Kunth) P.H. Raven, KC 141
Oenothera laciniata Hill, KC 33,66; JS 18261
Oenothera linifolia Nutt., JS, NS, WN, & AT 17976
Oenothera spachiana Torr. & A. Gray, JS & NS 17912
Oenothera speciosa Nutt., KC 36
Oenothera heterophylla Spach, JS, NS, WN, & AT 17972

OXALIDACEAE
Oxalis dillenii Jacq., KC 144, JS 18243
Oxalis violacea L., JS, NS, WN, & AT 17967

PASSIFLORACEAE
Passiflora incarnata L. , JS, NS, WN, & AT 17372

PLANTAGINACEAE
Plantago aristata Michx., KC 3, JS & NS 17911; JS 18252
Plantago elongata Pursh, JS, NS, WN, & AT 17301, JS 18494
Plantago pusilla Nutt., JS, NS, WN, & AT 17925
Plantago rhodosperma Decne., JS, NS, WN, & AT 17963
Plantago virginica L., JS, NS, WN, & AT 17364 & JS, NS, & WN 17334

POLEMONIACEAE
Phlox drummondii Hook., JS, NS, & WN 17317

POLYGONACEAE
Polygonum hydropiperoides Michx., KC 111, JS 18369
Rumex crispus L., JS, NS, WN, & AT 17929*
Rumex hastatulus Baldw., KC 35, 55, JS, NS, & WN 17342, JS 18480

PORTULACACEAE
Phemeranthus parviflorus (Nutt.) Kiger, KC 63
Portulaca pilosa L., JS & WN 17892, JS 18376
Portulaca umbraticola Kunth, JS & WN 17893

PRIMULACEAE
Anagallis arvensis L., JS, NS, WN, & AT 17389*
Anagallis minima (L.) Krause, JS, NS, WN, & AT 17310

RANUNCULACEAE
Clematis crispa L., KC 165, 166
Ranunculus pusillus Poir., JS, NS, WN, & AT 17940
Ranunculus laxicaulis (Torr. & Gray) Darby, KC 32
Ranunculus platensis Spreng., JS 18486

RHAMNACEAE
Berchemia scandens (Hill) K. Koch , JS, NS, WN, & AT 17381

ROSEACEAE
Crataegus crus-galli L., JS, NS, WN, & AT 17365
Crataegus marshallii Eggl., KC 113, JS, NS, WN, & AT 17345
Rosa bracteata J.C. Wendl., KC 163, JS, NS, WN, & AT 17345, JS & WN 17886
Rubus arguta Link, JS, NS, WN, & AT 17922
Rubus riograndis Bailey, JS, NS, WN, & AT 17326

RUBIACEAE
Diodia teres Walt., KC 80, JS 18406
Diodia virginiana L., KC 84, 97
Galium tinctorium L., JS, NS, WN, & AT 17368
Houstonia micrantha (Shinners) Terrell, JS, NS, WN, & AT 17301
Houstonia rosea (Raf.) Terrell, JS, NS, & WN 17303
Polypremum procumbens L., JS, NS, WN, & AT 17920
Stenaria nigricans (Lam.) Terrell, KC 70

RUTACEAE
Zanthoxylum clava-herculis L., JS, NS, WN, & AT 17373

SALICACEAE
Salix nigra Marsh., JS, NS, WN, & AT 17391

SAPOTACEAE
Sideroxylon lanuginosum Michx., JS, NS, WN, & AT 17949

SCROPHULARIACEAE
Agalinis heterophylla (Nutt.) Small ex Britton, KC 40, JS & WN 17894
Agalinis purpurea (L.) Pennell, JS 18375
Castilleja indivisa Engelm., KC 28
Gratiola flava, JS, NS, & WN 17321 & JS, NS, WN, & AT 17385
Gratiola brevifolia Raf., JS 18367
Gratiola neglecta Torr., JS 18255
Gratiola virginiana L., JS 18254

Lindernia dubia (L.) Pennell, JS, NS, & WN 17353
Nuttallanthus canadensis (L.) Sutton, JS, NS, WN, & AT 17953
Veronica peregrina L., JS, NS, & WN 17343

SOLANACEAE
Capsicum annuum L. var. *glabriusculum* (Dunal) Heiser & Pickersgill, KC 102*

ULMACEAE
Celtis laevigata Willd. JS, NS, WN, & AT 17392

URTICACEAE
Parietaria pensylvanica Muhl. ex Willd., JS, NS, & WN 17306
Urtica chamaedryoides Pursh, JS, NS, WN, & AT 17376

VALERIANACEAE
Valerianella florifera Shinners, JS, NS, WN, & AT 17369
Valerianella radiata (L.) Dufr., JS, NS, WN, & AT 17933, JS 18481

VERBENACEAE
Callicarpa americana L., JS, NS, WN, & AT 17395
Phyla lanceolata (Michx.) Greene, JS, NS, WN, & AT 17965
Phyla nodiflora (L.) Greene, KC 24
Verbena incompta P.W. Michael, KC 118, 125 *
Verbena halei Small, KC 2

VIOLACEAE
Viola affinis Leconte, JS, NS, & WN 17352

VITACEAE
Ampelopsis arborea (L.) Koehne, JS, NS, WN, & AT 17367
Vitis mustangensis Buckl., KC 57, 161

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A NEW SPECIES OF *EVOLVULUS* (CONVOLVULACEAE) FROM THE HIGH PLAINS OF THE TEXAS/NEW MEXICO BORDER

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ABSTRACT

Evolvulus arenarius Harms, **sp. nov.**, is described here. It is endemic to the High Plains sands of the Texas/New Mexico border region from Winkler Co., Texas, and Eddy Co., New Mexico, in the south to Hartley Co., Texas, and Curry Co., New Mexico, in the north. In some of these areas the new species is sympatric with the related *E. nuttallianus*. Some 15 collections of *E. arenarius* exist in Texas and New Mexico herbaria, where it has been identified as either *E. sericeus* or *E. nuttallianus*.

EVOLVULUS ARENARIUS Harms, **sp. nov.** TYPE: **USA. Texas.** Winkler Co.: Waddell Ranch, ca. 11 mi ENE of Kermit, N of Texas Hwy 302, in deep sand among *Quercus havardii*, 2800 ft, 7 Jun 1950, *B.H. Warnock & J.O. Parks 8773* (holotype: TEX 00295128!; isotype: SRSC!). (Fig. 1)

Similar to *Evolvulus nuttallianus* Schult. in its pentastichous phyllotaxis, pinnate venation, vestiture consisting of thick hairs on both leaf surfaces, and lavender flowers at anthesis; different in its slender, open habit (Figs. 2, 3), leaves narrowly linear, with sparse vestiture, leaves with slightly denser pubescence on the upper surface, consisting of hairs more strongly asymmetrically forked (short branch <0.25 mm), flowers turning yellow with age, and ovate sepals. Similar to *E. sericeus* Sw. in its slender habit (Fig. 3), ovate sepals and flowers yellowing with age; differing in leaf orientation, phyllotaxis, venation, vestiture, and flower color at anthesis.

In the description below character states that differ significantly between *Evolvulus arenarius* and *E. nuttallianus* are highlighted in italic bold.

Perennial herbs. **Stems** ascending, 8–30 (43) cm long, 0.7–1.1 in diameter at the base, at mid stem 0.4–0.8 mm, branched at the base with limited branching above, also with ***long subterranean stems***. Phyllotaxis pentastichous 5/2 (Fig. 4). ***Foliage not dense, mid stem internodes 2–10 mm*** (67% > 4 mm in a sample of 30) (Figs. 5–7). **Leaves** oriented toward the branch tip from their base, margin entire, ***mid stem blades linear to narrowly elliptical***, 8–15.5 mm long, 0.8–1.4 mm wide, ***length/width ratio 1:8.1–1:12.2***, leaf apex acute, base cuneate, petiole < 1 mm if present and poorly differentiated, venation pinnate (visible only with clearing) with a strong midvein (Figs. 8–9). **Vestiture** of stems and leaves similar, consisting of ***sparse appressed hairs*** (Fig. 12), strongly tawny to silver-gray (even on the same leaf), aligned parallel with the midrib, ***denser on upper surface*** (Fig. 13), thick (not sericeus) and ***strongly asymmetrically forked*** (Figs. 14–16), stalkless, with two concentric basal cells (Fig. 18), slightly spreading and tapering from the connecting base to acute tips, ***the weak fork (0.08) 0.1–0.25 (0.3) mm long***, the strong fork (0.4) 0.6–1.5 mm long with max. hair width 19.6 µm; max. hair width at the base of the weak fork ca. 70% of that of the adjacent strong fork (Figs. 17–18). **Flowers** solitary at the nodes, primarily in central portions. **Peduncles** absent. **Pedicels** 1–4 mm at anthesis, lengthening and recurved in fruit. ***Outermost two sepals ovate*** with an acute tip, 3.1–4.1 mm long, ***±1 mm wide 1 mm from the base*** (Figs. 19-20), ***scant hairs on the distal inner surface***. **Corolla** rotate, 9.2–14 mm in diameter (in dried specimens), the lower tube ± 2.5 mm long; interplicae paler than plicae and pubescent on the outside distal half; corolla color in shades of

lavender at anthesis, paler in the throat, ***yellowing with age***, interplicae fading first (Figs. 21–22). **Filaments** to 3.2 mm long; anthers 0.7–0.9 mm long. Styles exceeding the anthers, with 2 branches 2–3 mm long. **Capsule** subglobose, tan, dehiscing by valves, circumscissile. **Seeds** dark brown, smooth, globose, ca. 0.8 mm in diameter.

Blooming from late May to early September (earliest collection 23 May, latest 2 Sep). In deep sand, grasslands, scrub (especially *Quercus havardii*). Endemic to the High Plains sands (Shinnery Sands & Rolling Sand Plains and immediately adjacent areas) of the Texas/New Mexico border from Winkler Co., Texas, and Eddy Co., New Mexico, in the south to Hartley Co., Texas, and Curry Co., New Mexico, in the north (Fig. 23).

Additional collections examined. **New Mexico**. Curry Co.: 18 mi NW of Melrose, 14 Jul 1951, *Clark s.n.* (NMU). Eddy Co.: Los Medanos Site near Carlsbad, 32.34805 -103.78270, 15 Jun 1978, *Marley s.n* (NMU); 0.5 mi N of James Ranch, 32.31909 -103.81690, 29 Jun 1978, *Marley, Knight, Martin, and Powell s.n* (NMU). Roosevelt Co.: Melrose Air Force Range, 2 mi due N of mesa top installation, 1.5 mi E of Krider Rd, Springer loamy fine sand, slope: 3 degrees, aspect: 15 degrees azimuth, elev. 1314 m, 14 Jun 1994, *Bleakly & DeBruin 546* (NMU); N of Causey, 31 Jul 1938, *Castetter 10693* (NMU); ENMU Natural History Preserve, elev. 4000 ft, 4 Aug 1971, *Secor 73* (TEX); Milnesand Prairie Preserve, W side of hwy pasture near natural gas well, grass dominated area, swale present dominated by *Eleocharis* sp., *Bouteloua hirsuta*, *B. curtipendula*, *Eragrostis curvula*, *Paronychia jamesii*, *Lmum berlanderieri* associated, N33 40.654 W103 21.921, 26 Aug 2006, *Strahan 473* (NMCR); Parkinson Ranch, Milnesand, *Quercus havardii/Schizachyrium scoparium - Boutelous hirsuta* shrubland, UTM 663524 E 3722719 N NAD83 Zone 13, elev. 4100 ft, 7 Aug 2007, *Chauvin 07GC001-F34* (NMU). **Texas**. Andrews Co.: Survey site #1, dry sandy soil, 23 May 1962, *Adv. Bio. Class s.n.* (SRSC). Gaines Co.: 4 mi of Seminole, 10 Jul 1941, *Tharp s.n.* (TEX). Hartley Co.: 2 mi SW of Dalhart, red sand sage, 19 Jun 1936, *McMurry s.n.* (TEX). Winkler Co.: 10 mi E of Kermit on Hwy 302, infrequent in sandy soil, 4 Aug 1952, *McCullough 320* (SRSC); Waddell Ranch, E of Kermit, sparse among shinney deep sand, 7 Jun 1950, *Warnock & Parks 8773* (SRSC, TEX).

Although not seen, there is reason to believe that *K.W. & L. Allred 9437* (NMCR; Chaves Co., New Mexico), originally identified as *Evolvulus sericeus*, may also represent *E. arenarius*.

In late June I was able to visit Winkler and Andrews counties to search for *Evolvulus arenarius*. We did not have access to ranches or other sites in the area, so my daughter Kirsti and I started from the roadside along the Waddell Ranch some 10 miles east of Kermit, the site of Warnock's type collection and of *McCullough 320* (SRSC). We walked the roadside on two highways through the shinnery sands east of Kermit for the whole morning, but without luck. The area had been in extreme drought for over a year and only recently had some rains (Figs. 25–28).

Relevant *E. muttalliamus* specimens examined. **Colorado**. Baca Co.: Springfield, Two Buttes Cr. 14 mi N, 4300 ft., ***dry sandy soil*** in sun on hill top, prairie grassland, 9 Jun 1948, *Taylor 38* (TEX). Yuma Co.: J. Conrad property, N of Wray, 5.5 mi N of Hwy 34, 1 mi E of County rd BB, T2N R44W S7, 3800 ft, ***sand hills***, 8 Jun 1988, *Neely 5062* (TEX); ***sand hills*** due E of Arikaree River, 1.25 mi NE of Willow Creek Ranch, T1S R42W S27, 3450 ft., N-facing slope, ***sand hills***, 9 Jun 1988, *Neely 5081* (TEX); **New Mexico**. Eddy Co.: The Divide, 15-May-87, *Cockman 87-70* (NMC). Harding Co.: Black Hills at pass through hills on State Rd. 65 ca. 0.8 mi E of State Rd. 102, 35.83856°N 103.66159°W, elev. 4490 ft, ***sandy clay hill*** slope with basalt cobble, 24-Aug-08, *Sivinski 6969* (NMU). Lea Co.: Los Medanos, T22S, R32E sec 9 (SE 1/4) A-3 S edge of divide quarry area, elev. ca. 3800 ft, 15-Jun-78, *Marley, Knight, Martin, & Powell 1458* (NMU); Quay Co.: Tucumcari, roadside, elev. 4200 ft, 20-Jun-31, *Castetter 7362* (NMU). Roosevelt Co.: Melrose Air Force Range, 2

mi due N of mesa top installation, 1.5 mi E of Krider Rd, ***Springer loamy fine sand***, slope: 3 degrees, aspect: 15 degrees azimuth, elev. 1314 m, 3 May 1993, *Bleakly & DeBrum 12* (NMU); ENMU Natural History Preserve, Portales (Bouteloua-Buchloe Grassland), elev. 4000 ft, 8 May 1970, *Secor 12* (TEX); ENMU Natural History Preserve, Portales (short-grass prairie), ***sandy soil***, elev. 4000 ft, 19 May 1973, *Secor 14* (TEX). **Texas**. Andrews Co.: city of Andrews, common on vacant lots, 20 May 1962, *Adv. Bio. Class s.n.* (SRSC). Bailey Co.: near Muleshoe, 14 Jun 1929, *B.C. Tharp s.n.* (TEX). Cochran Co.: ca. 2 mi N of Bledsoe along hwy 595, ***red sandy soils***, 16 May 2000, *B.L. Turner & M. Turner 20-238* (TEX); ca. 2 mi N of Bledsoe along hwy 595, ***red sandy soils***, 16 May 2000, *B.L. Turner & M. Turner 20-238* (TEX). Crockett Co.: Hwy 163 3 1/2 mi N of Ozona in the NE part of the county, elev. 2300 ft, 21 Apr 1964, *Read 599* (SRSC). Culberson Co.: McKittrick Canyon, Guadalupe Mountains, elev. 6500 ft, 22 May 73, *Warnock 21506* (SRSC); Manzanita Spring, Guadalupe Natl. Park, 519065 E 3530637 N NAD83 Zone 13, elev. 5571 ft, aspect 115, slope 5%, rock type limestone, *Juniperus pinchotii/Muhlenbergia setifolia* shrubland, 26 Aug 2006, *Chauvin 06YC198-FS* (NMU); eastern foothills of Guadalupe Mts., 3 mi E of Nickel Creek, 15 Jul 1945, *Muller 8255* (LL). Dallam Co.: Rte. 1879, 6-10 mi S of Rte. 296, dry roadside ***on dune sand***, 8 Jul 1963, *Correll & Ogden 28390* (TEX). Donley Co.: Conchas Dam, Davis Mountains, elev. 4000 ft, 2 Jun 1957, *Correll 16576* (LL). Hudspeth Co.: head of Victoria Canyon, Sierra Diablo, at T.A. Beards lodge, elev. 3500 ft, on limestone soil, infrequent, 18 Aug 1953, *Warnock 11426* (SRSC); **Utah**. Kane Co.: ***very sandy soil around the edge of big sand dune*** 1.5 mi E of the Paria River and 12 mi W of Glen Canyon City, 45 mi E of Kanab, Twp. 43 W, R 1 W, S 2, elev. ca. 4500 ft, plants deep-rooted, and also with slender, creeping roots, flowers lavender, 23 May 1965, *Cronquist 10174* (TEX).

Relevant *E. sericeus* specimens examined. **New Mexico**. Catron Co.: Apache National Forest, Saddle Mountain region, next to bridge that crosses Pueblo Creek near the campground, N33d35.51' W108d57.74', 7 Aug 2001, *Johnson 604* (NMCR). Eddy Co.: Queen, elev. 5900 ft., 1 Aug 1909, *Wooton s.n.* (NMC); Dark Canyon along FSR 69, 2.8 air mi E of Klondyke Gap, 32° 07.359' N 104° 43.283' W, 5850 ft., 10 Jul 2010, *Worthington 36166* (SRSC). San Miguel Co.: Las Vegas, 13 Mar 1905, *Cockerell s.n.* (NMC); Conchas Dam E of north campground, elev. 4000 ft., 12 Nov 1965, *Broeske MO-6* (NMU); Conchas Dam, Davis Mountains, elev. 4000 ft., 12 Nov 1965, *Broeske MO-65* (NMU). **Texas**. Jeff Davis Co.: jct of Goat and Merrill Canyons about 5 mi SW of Mt. Livermore, elev. ca. 5500 ft, on dry exposed gentle slopes, 30 Jul 1935, *Hinckley 234* (LL).

The contrasts below distinguish *Evolvulus arenarius* from *E. nuttalliamus* and *E. sericeus* in trans-Pecos Texas and New Mexico. All three can have hairs on both leaf surfaces, but forms of *E. sericeus* may have the upper surface glabrous.

1. Leaves spreading, upper leaves often falcate and conduplicate (may be pressed flat when mounted), phyllotaxis distichous, venation palmatipinnate (one or more pairs of secondary veins from the base parallel to the leaf margin to the midpoint of the leaf or higher, pinnate secondaries only above the midpoint); hairs fine (sericeous) ..... **Evolvulus sericeus**
1. Leaves erect and typically bent upward at attachment, upper leaves typically flat or broadly u-shaped, phyllotaxis pentastichous 5/2, venation pinnate, hairs stout.

   2. Foliage sparse with internodes commonly > 4 mm, mid leaves linear, length/width ratio > 8:1; hair strongly asymmetrical with weak forks < 0.25 mm long, hairs denser on upper surface, outermost sepals ovate; corolla yellowing with age ..... **Evolvulus arenarius**
   2. Foliage dense with internodes rarely > 4 mm, mid leaves elliptical, length/width ratio < 8:1, hair weakly asymmetrical with weak forks > 0.25 mm long, hairs denser on lower surface, outermost sepals lanceolate; corolla not turning yellow with age ..... **Evolvulus nuttallianus**

The new species has been confused with both *Evolvulus sericeus*, especially due to the narrow leaves and open habit, and *E. nuttallianus*, which shares with *E. arenarius* several critical character states not found in *E. sericeus*, as outlined in the diagnosis above. While the new species has some character states of each of these two species, the possibility that it represents a hybrid seems remote on morphological, ecological, and distributional grounds. Hair type in *E. arenarius* (Fig. 15) is different from either of the other two species and in no way intermediate. The new species is restricted to deep sands, not a habitat "intermediate" between that of the other two species, and through most of its range it is sympatric with only *E. nuttallianus*.

The possibility that *Evolvulus arenarius* is an environmentally triggered form (or variety) of *E. nuttallianus* was seriously considered. It has clearly adapted to its deep sand ecology, with longer internodes and long subterranean stems. And it shares the venation and phyllotaxis of *E. nuttallianus,* which suggests a close relationship.

On the other hand, it is sympatric with *Evolvulus nuttallianus* in the same deep sand environments and locales; e.g., *Bleakly & DeBrum 546* & *12* (NMU) represent both taxa at the same location in Roosevelt Co., New Mexico, with the ecological information "soil: Springer loamy fine sand, slope: 3 degrees" (Fig. 2); similarly *Secor 73* & *12* (TEX), at the ENMU Natural History Preserve in Roosevelt Co. (Fig. 3), and Robert Strahan's collection at Milnesand Prarie (*473*) is matched with his photograph of *E. nuttallianus* from that site (Strahan 2008). Sand and dune collections of *E. nuttallianus* were examined for all sites for which collections were available; e.g., "Sand hills due E of Arikaree River", Yuma Co., Colorado, *Neely 5081* (TEX) and "Very sandy soil around the edge of big sand dune," Kane Co., Utah, *Cronquist 10174* (TEX). All of these specimens have typical *E. nuttallianus* features, contrasting with *E. arenarius*.

Where they are sympatric and both have been collected by the same person, they have been identified as different taxa, reflecting a sense that they are not the same, with *E. arenarius* being labeled *E. sericeus*, the only other option in available *Evolvulus* keys. In general, the type specimens and 5 others were originally determined as *E. nuttallianus*, while 7 other specimens were identified as *E. sericeus*. The labels on several indicate some hesitance in assigning a species epithet (Fig. 24).

Features not shared with *Evolvulus nuttallianus* that cannot easily be attributed to environmental forces are (1) ovate outer sepals, (2) corolla turning yellowish with age, (3) overall sparse pubescence, with denser hairs on the upper leaf surface, and (4) the strong reduction in trichome length of the weak fork.

Sepal differences have played a significant role in distinguishing *Evolvulus sericeus* and *E. nuttallianus,* from Nuttall's 1818 description of *E. pilosus* Nutt. (an illegitimate name for *E. nuttallianus* Schult.) to the present. Van Ooststroom's 1934 monograph (pp. 101–103) distinguishes *E. pilosus* (i.e., *E. nuttallianus*) as having lanceolate or narrow-lanceolate sepals; *E. sericeus* with narrow-oblong-lanceolate to oblong-lanceolate sepals. The five sepals of *Evolvulus* are quite different in overall form (equal to subequal only if length is considered). Only the outermost two sepals show the critical form for distinguishing taxa. Determining sepal morphology with pressed, mounted specimens can be challenging but an outer sepal can generally be found.

Leaf venation

Leaf venation in *Evolulus* presents useful taxonomic characters, but its study and use is complicated by two factors. First, *Evolvulus* leaves are characterized by low (1r) "leaf rank", as defined by the Leaf Architecture Working Group (1999). This means that the level of organization of the leaf venation is relatively low, with vein course and other characteristics often more or less irregular, and the petiole (as is the case in *Evolvulus*) often not strongly differentiated from the

lamina. Differences in venation between species, when they exist, are thus more on the level of tendencies than absolute differences, and details can vary from leaf to leaf.

Secondly, leaf venation in the *Evolvulus* species under study here is often not easily determined, especially when obscured by pubescence. It was studied in two ways: (1) leaf clearing and (2) shining a bright light through a rehydrated or fresh leaf, using a slide scanner. Samples of *E. arenarius, E. nuttallianus,* and *E. sericeus* leaves were cleared using a 1% aqueous solution of basic fuchsin to which 10 gm of solid NaOH had been added. The leaves were then processed for mounting on slides with Permount. Detailed venation patterns were then photographed using a dissecting microscope with SPOT 4.6 software. Both *E. nuttallianus* (Fig. 10) and *E. arenarius* (Fig. 8) showed pinnate venation. With *E. sericeus* venation was palmatipinnate (Figs. 9, 11) — one or more pairs of secondary veins from the base parallel to the leaf margin to the midpoint of the leaf or higher; pinnate secondaries only above the midpoint. These studies will be detailed in a separate publication.

Rehydrated leaves were also imaged as 'transparencies' using an Epson Perfection flatbed slide scanner. Leaves of *Evolvulus sericeus* have relatively good light transmittance, revealing secondary veins, even for the narrowest (ca. 1.5 mm wide) leaves (Fig. 11G-H). Both *E. nuttallianus* (Fig. 10C-D) and *E. arenarius* have very weak light transmittance, with secondary veins not clearly visible.

Hair morphology

A study of *Evolvulus* hair morphology seemed appropriate in view of the distinctive vestiture of *E. arenarius* collections. With a dissecting microscope at higher magnification, entire individual trichomes are readily discerned (unlike the 'spagettiform' vestiture of *E. nuttallianus*), and the fork asymmetry is apparent, although the slightly erect angle of the very short weak fork often made it difficult to see. To examine the hairs in more detail one leaf was taken from TEX/LL and SRSC specimens from Roosevelt Co., New Mexico, Winkler Co., Texas, Andrews Co., Tesax, Gaines Co., Texas, and Yuma Co., Colorado. Two approaches were applied: (1) extracted trichomes were viewed with light microscopes and (2) small leaf samples were scanned by SEM.

For light microscope examination a sampling of hairs was scraped off both surfaces with a sharp razor into a drop of water containing a small amount of Aerosol OT Solution as wetting agent onto a glass slide and then covered with a cover glass. These were immediately photographed with a dissecting microscope. This procedure was applied to leaves of (1) *Evolvulus arenarius* from Winkler Co., Texas, Gaines Co., Texas, and Roosevelt Co., New Mexico; (2) *E. nuttallianus* from Roosevelt Co., New Mexico, Donley Co., Texas, and Culberson Co., Texas; and (3) with *E. sericeus* leaves from various collections in the Davis Mountains, the closest area in Texas for which they were available. With *E. sericeus* I examined hairs from specimens with a glabrous upper surface and from those with hairs on both surfaces. Only with *E. sericeus* were the hairs found to be different on the two surfaces.

SEM images were made for a limited selection for *Evolvulus arenarius* (Winkler Co., Texas, TYPE), *E. nuttallianus,* Culberson Co., Texas, and *E. sericeus*, Jeff Davis Co., Texas. Small leaf sections (±1 mm) mounted on aluminum stubs were sputter coated with platinum. Scans were made at 800x for hair arrangement and density and at 2000x & 6000x with 45° tilt to show trichome base features *in situ* (not possible with scraped hairs).

Evolvulus nuttallianus in the sand areas has strong fork lengths and asymmetrical trichome widths similar to *E. arenarius*, but with longer weak forks commonly having max. lengths to 0.5 mm long. For *E. sericeus* the hairs were typically narrower and both forks longer — but width at the base does not permit distinguishing a weak and strong fork even when the widths differ (Fig. 15).

ACKNOWLEDGEMENTS

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Figure 1 *Evolvulus arenarius*, holotype

Figure 2. *Evolvulus arenarius, Bleakly & DeBruin 546* (NMU) (left) and *E. nuttallianus. Bleakly & DeBruin 12* (NMU), both in "Springer loamy fine sand" at Melrose Air Force Range in Roosevelt Co., New Mexico.

Figure 3. Left *Evolvulus arenarius, Secor 73* (TEX), Mid. *E. nuttallianus. Secor 12* (TEX), both from ENMU Natural History Preserve in Roosevelt Co., New Mexico, Right *E. sericeus, Worthington 36166* (SRSC), Eddy Co., New Mexico. Eddy is the only county with *E. arenarius* as well as *E. sericeus* collections, the latter from the Guadalupe Mts. in the SW corner.

Figure 4 *Evolvulus arenarius* Pentastichous 5/2 leaf arrangement, with leaf orientation toward the stem apex View A [top] consists of the segments D, C, B, read bottom up *Warnock & Parks 8773* (TEX)

Figure 5 *Evolvulus arenarius* 5 cm section of mid leaves of *Warnock & Parks 8773* (TEX)

Figure 6. *Evolvulus arenarius*. 5 cm section of mid leaves of *Bleakly & DeBruin 546* (NMU, Roosevelt Co., New Mexico) ["Soil: Springer loamy fine sand"]

Figure 7. *Evolvulus nuttallianus*. 5 cm section of mid leaves of *Bleakly & DeBruin 12* (NMU, Roosevelt Co., New Mexico) ["Soil: Springer loamy fine sand"]

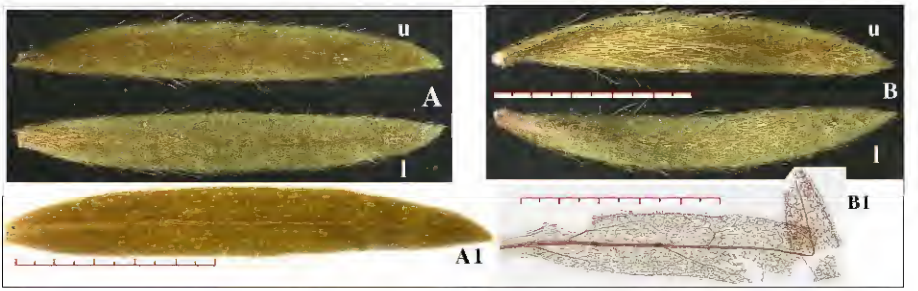

Figure 8. *Evolvulus arenarius*. A: leaf 1; u: upper surface; l: lower surface; A1: leaf 1 rehydrated for transparency scanning of venation; B: leaf 2; B1: leaf 2 venation after clearing & staining. *Warnock & Parks 8773* (TEX).

Figure 9. Transparency scan of flattened *Evolvulus sericeus* narrow leaf showing palmatipinnate venation.

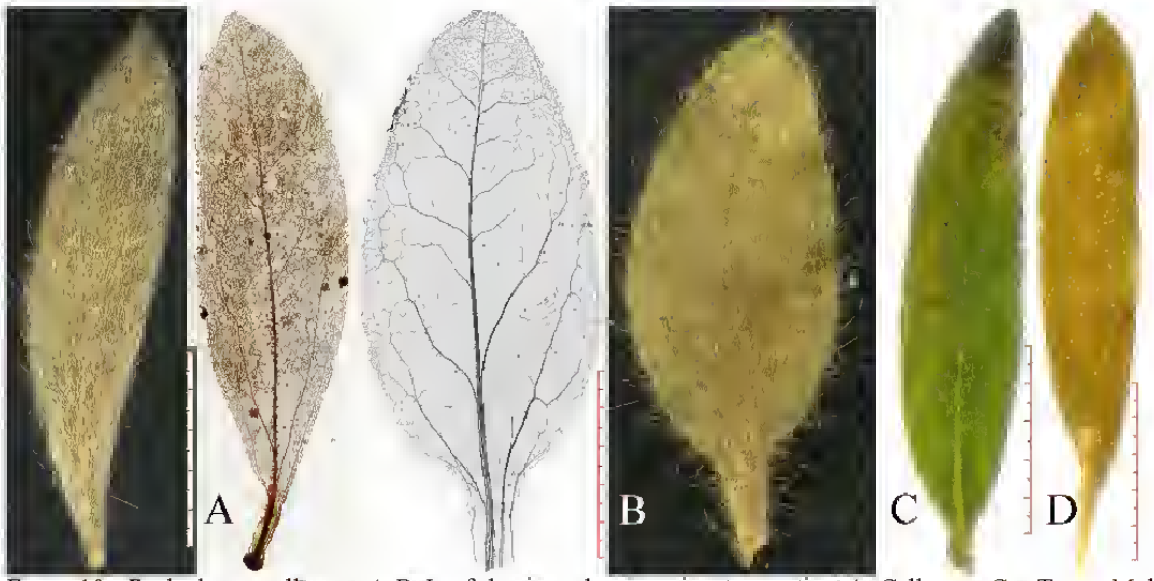

Figure 10. *Evolvulus nuttallianus*. A-B: Leaf clearings showing pinnate venation, A: Culberson Co., Texas, *Muller 8255* (LL), B: Kane Co., Utah, *Cronquist 10174* (TEX); C-D: Transparency scans, C: fresh leaf, Hays Co., Texas, D: rehydrated leaf, Dallas Co., Texas, *Lundell & Lundell 10618* (LL)

Figure 11. *Evolvulus sericeus*. E-F: Leaf clearings showing palmatipinnate venation, E: Jeff Davis, Co., Texas, *Harms et al. 109* (TEX), F: Brewster Co., Texas, *Warnock 21472* (TEX); G-H: Transparency scans; G: fresh leaf, Hays Co., Texas; H: rehydrated, with insert showing dense hairs of 1 mm section of lower surface (L) & upper surface (U), Presidio Co., Texas, *Carr 31161* (TEX)

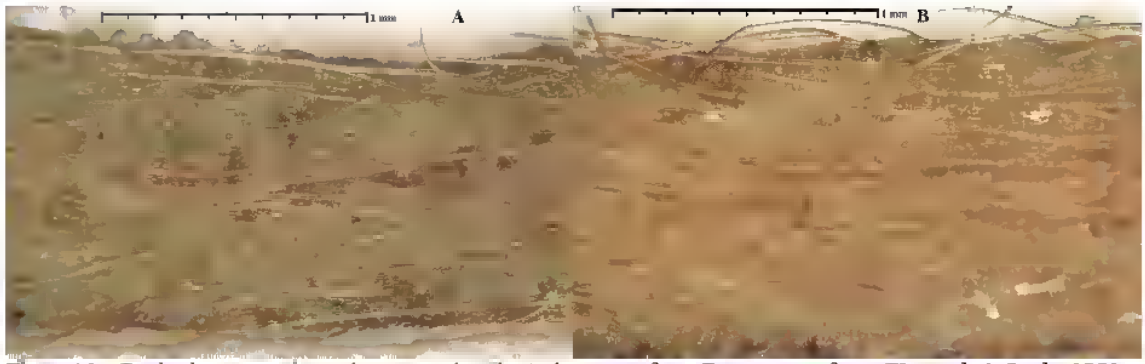

Figure12 *Evolvulus arenarius* pubescence detail. A. lower surface, B. upper surface *Warnock & Parks 8773* (TEX)

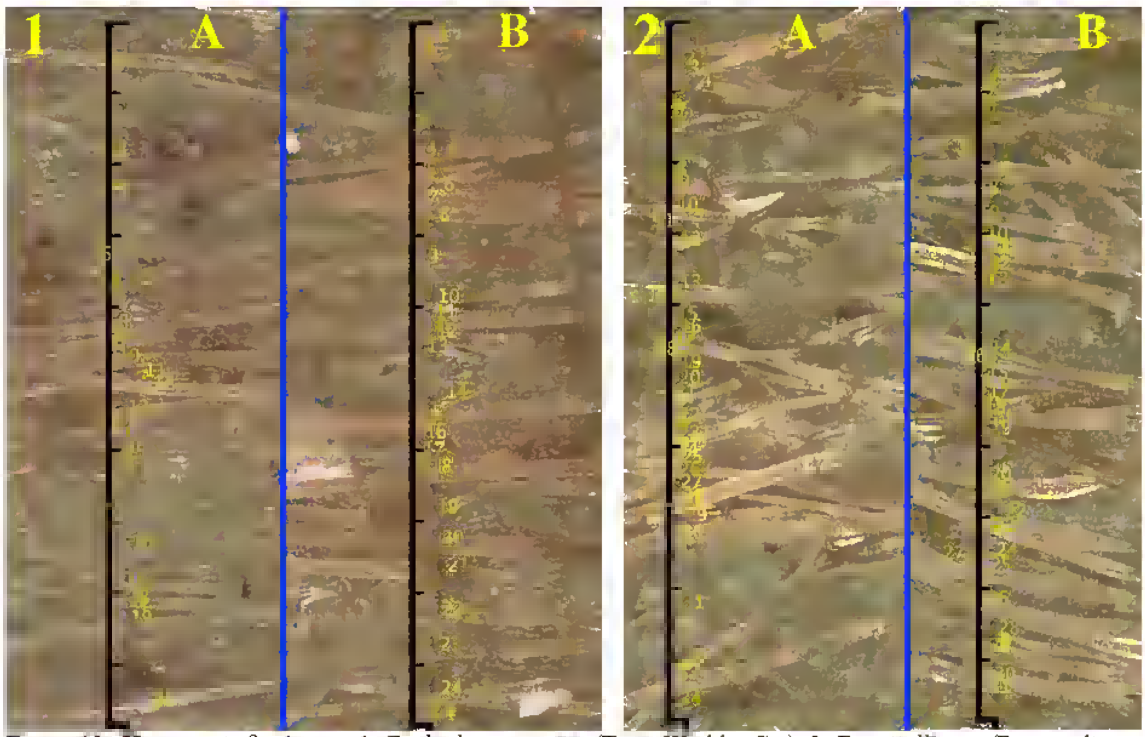

Figure 13. Hair counts for 1 mm. 1. *Evolvulus arenarius* (Type, Winkler Co.), 2. *E. nuttallianus* (Roosevelt Co.); A. Lower surface, B. Upper surface.

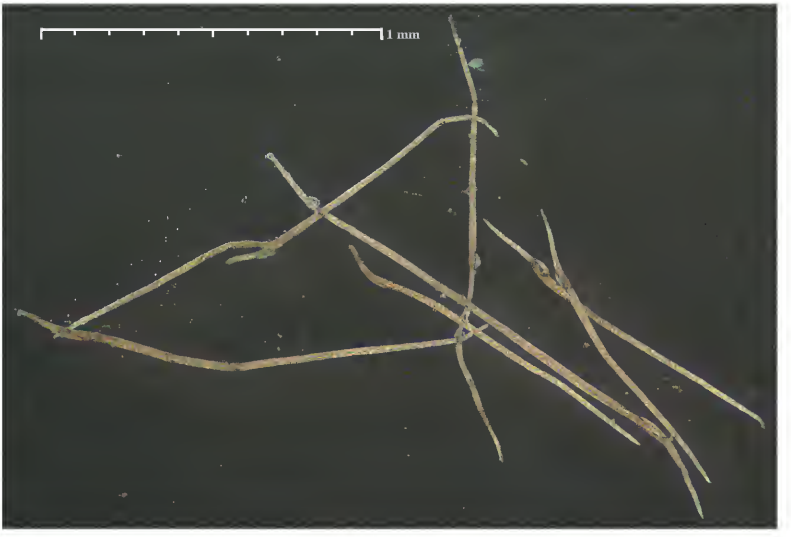

Figure 14. *Evolvulus arenarius* asymmetrical bifurcate hairs. *Warnock & Parks 8773* (TEX).

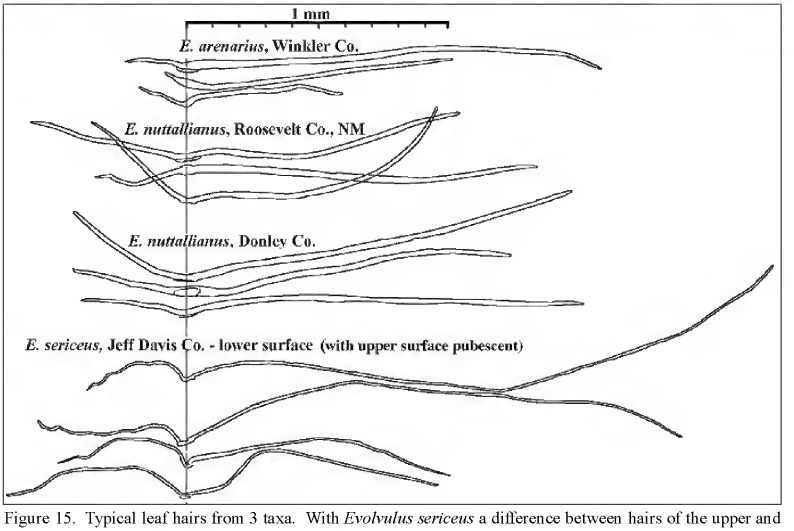

Figure 15. Typical leaf hairs from 3 taxa. With *Evolvulus sericeus* a difference between hairs of the upper and lower surface was noted. Vertical line indicates the base (point of attachment), with the weak fork to its left.

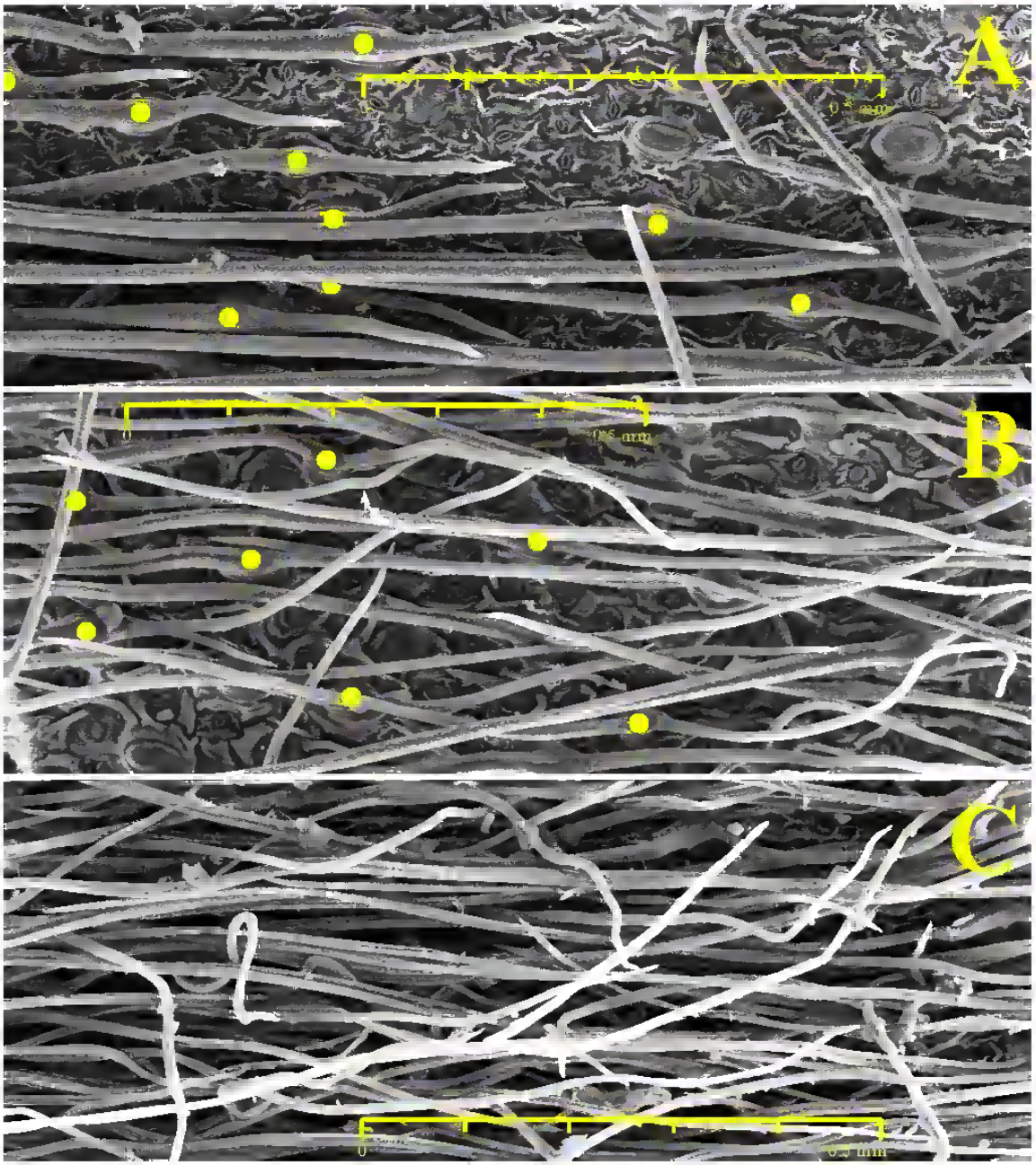

Figure 16. SEM images of leaf surfaces for A: *Evolvulus arenarius*, Winkler Co., Texas (holotype), B: *E. nuttallianus*, Culberson Co., Texas, C *E. sericeus*, Jeff Davis Co., Texas Scanned at 800 x. Yellow dots at trichome base for hairs having the full length of weak forks visible. None were apparent in the dense hairs of *E. sericeus*.

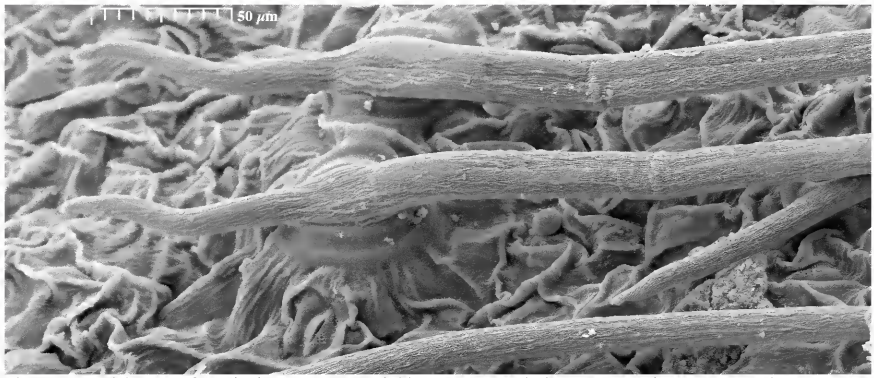

Figure 17. Trichomes of *Evolvulus arenarius*, Winkler Co., Texas (holotype), SEM images scanned at 6000 x, 45° tilt.

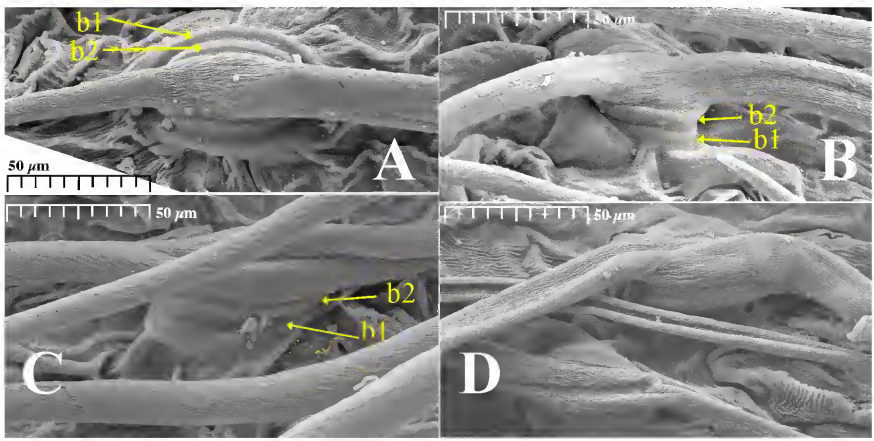

Figure 18. SEM images of concentric trichome basal cells (b1, b2) for A: *Evolvulus arenarius*, Winkler Co., Texas (holotype); B-C: *E. nuttallianus*; B: Culberson Co., Texas; C: Yuma Co., Colorado; D: single cell trichome base of *E. sericeus,* Jeff Davis Co., Texas. Scanned at 6000 x, 45° tilt.

Figure 19. Sepal comparison. Roosevelt Co., New Mexico. Left: *Evolvulus arenarius, Secor 73* (TEX); right: *E. nuttallianus, Secor 12* (TEX).

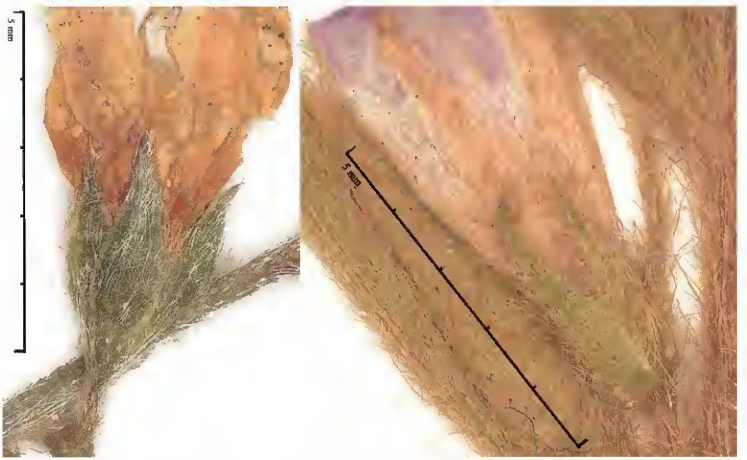

Figure 20. Sepal comparison. Left: *Evolvulus arenarius,* Winkler Co., Texas, *McCullough 320* (SRSC); right: *E. nuttallianus,* Andrews Co., Texas, *Adv. Bio. Class s.n.* (SRSC).

Figure 21. *Evolvulus arenarius* corolla, Eddy Co., New Mexico, *Marley s.n.* (NMU); yellowing, Roosevelt Co., New Mexico, *Strahan 473* (NMCR).

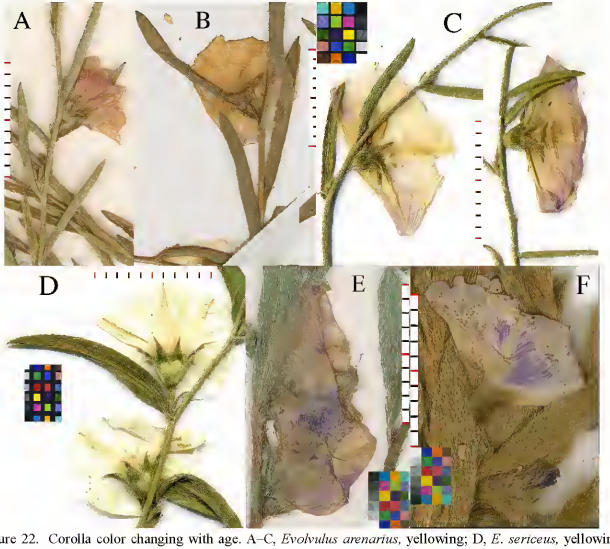

Figure 22. Corolla color changing with age. A–C, *Evolvulus arenarius,* yellowing; D, *E. sericeus,* yellowing; E–F: *E. nuttallianus,* losing color; A: Winkler Co., Texas, *Warnock & Parks 8773* (TEX); B: Gaines Co., Texas, *Tharp s.n.* (TEX); C: Roosevelt Co., New Mexico, *Strahan 473* (NMCR); D: Catron Co., New Mexico, *Johnson 604* (NMCR); E: Harding Co., New Mexico, *Sivinski 6969* (NMU); F: Crockett Co., Texas, *Read 599* (SRSC).

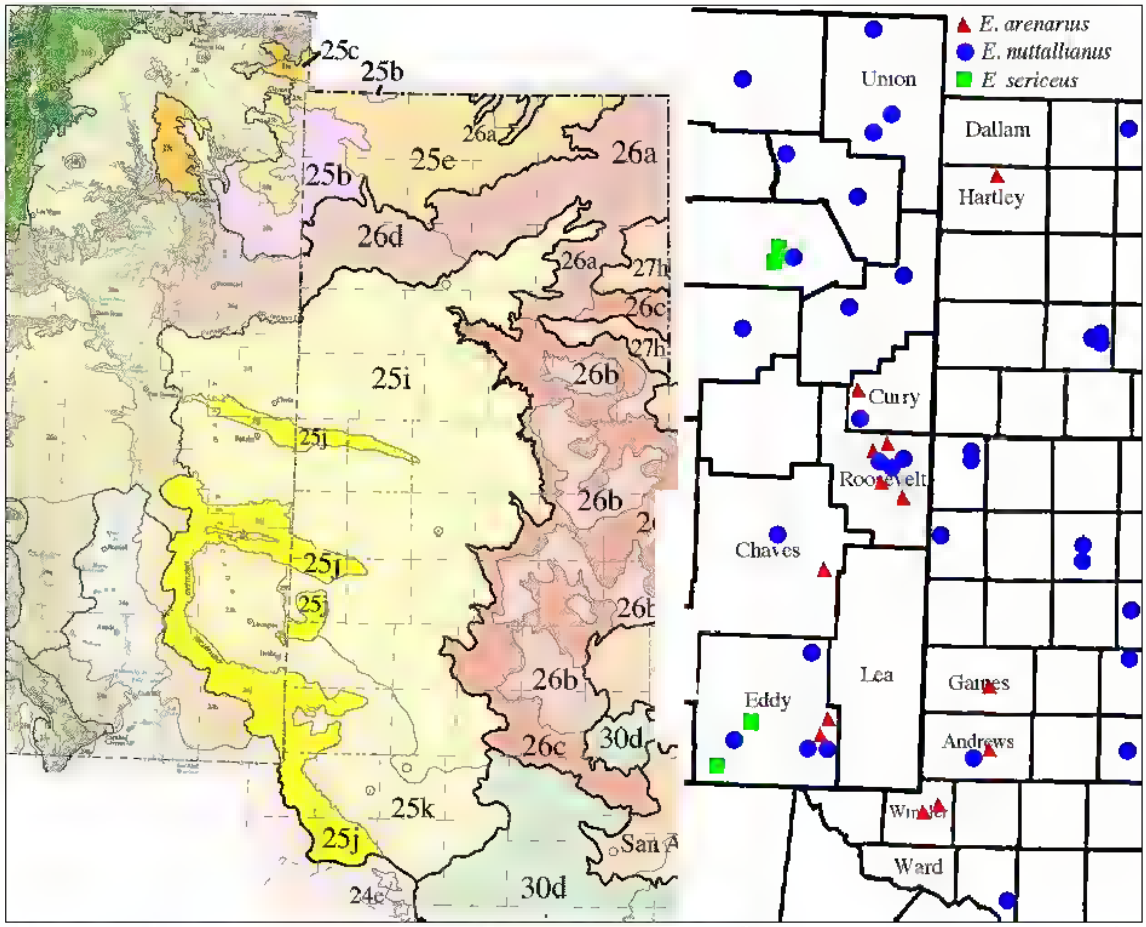

Figure 23. High Plains along the New Mexico–Texas border, areas indexed '25b–k'. *Evolvulus arenarius* occurs in areas 25j (Shinnery Sands) & 25b (Rolling Sand Plains) and immediately adjacent areas. Ecoregions are adapted from Griffith et al (2006 & 2007) and Strahan (2008).

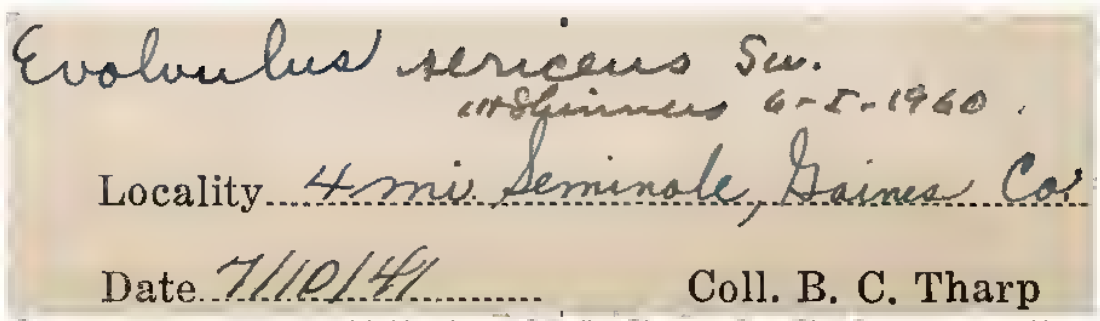

Figure 24. TEX 00026512, 1941 label by Tharp, originally with no species epithet; in 1960 annotated by Shinners as *Evolvulus sericeus*, subsequently placed with *E. nuttallianus* collections.

Figure 25. Shinnery oaks on the Waddell Ranch, 10 miles E of Kermit along State 302, Winkler Co., Texas, 23 June 2013. The type of *Evolvulus arenarius* was collected from this ranch.

Figure 26. Roadside 9 miles E of Kermit along State 115, Winkler Co., Texas, 23 June 2013.

Figure 27. Dunes along roadside 9 miles E of Kermit along State 115, Winkler Co , Texas, 23 June 2013

Figure 28. Roadside 9 miles E of Kermit along State 115, Winkler Co., Texas, 23 June 2013.

Angelo, R. and D.E. Boufford. 2014. Atlas of the flora of New England: Families of vols. 17 & 18: Flora of North America. Phytoneuron 2014-21: 1–24 + map pages 1–32. Published 28 January 2014. ISSN 2153 733X

ATLAS OF THE FLORA OF NEW ENGLAND: FAMILIES OF VOLS. 17 & 18: FLORA OF NORTH AMERICA

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ABSTRACT

Dot maps are provided to depict the distribution at the county level of the taxa of Magnoliophyta: Families of volumes 17 and 18 of Flora of North America growing outside of cultivation in the six New England states of the northeastern United States. Families included are Adoxaceae, Aquifoliaceae, Campanulaceae, Caprifoliaceae, Lentibulariaceae, Orobanchaceae, Plantaginaceae, Rubiaceae, and Scrophulariaceae (Aquifoliales, Asterales, Dipsacales, Gentianales, Lamiales). The maps treat 274 taxa (species, subspecies, varieties, and hybrids, but not forms) based primarily on specimens in the major herbaria of Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut, with most data derived from the holdings of the New England Botanical Club Herbarium (NEBC). Brief synonymy (to account for names used in standard manuals and floras for the area and on herbarium specimens), habitat, chromosome information, and common names are also provided.

This article is the thirteenth in a series (Angelo & Boufford 1996, 1998, 2000, 2007, 2010, 2011a, 2011b, 2012a, 2012b, 2012c, 2013a, 2013b) that presents the distributions of the vascular flora of New England in the form of dot distribution maps at the county level (Figure 1). Two more articles are planned. The atlas is posted on the internet at <http://neatlas.org>, where it will be updated as new information becomes available.

This project encompasses all vascular plants (lycophytes, pteridophytes and spermatophytes) at the rank of species, subspecies, and variety growing and established independent of cultivation in the six New England states. Hybrids are also included, but forms and other ranks below the level of variety are not. The dots are based on voucher specimens primarily in New England herbaria (of colleges, universities, botanical gardens, and public museums) representing reproducing populations outside of cultivated habitats. This thirteenth installment includes the families that will be included in volumes 17 and 18 of the Flora of North America North of Mexico. Of the 274 taxa treated, 127 are not native to the region. Future accounts will treat the distribution of additional non-monocot angiosperms.

The habitat data are distillations from a variety of sources augmented by our own field observations. An attempt was made to indicate habitat information as it applies to a particular taxon in New England rather than to the entire range of the taxon. Habitat information is not provided for hybrid taxa.

It is our hope that these articles will stimulate additional field work to supplement the distributions portrayed in the maps. The New England Botanical Club herbarium has proven to be the most important resource for this project. We are eager to receive information on voucher specimens in public herbaria documenting range extensions and filling county gaps in distributions. Similarly, because the atlas of the New England flora will be continuously updated as new information becomes

available, we are eager to receive notification of published corrections of cytological information and new, documented chromosome counts for taxa in the New England flora.

MATERIALS AND METHODS

Materials and methods are as outlined in Angelo and Boufford (1996) and in a web version (Angelo & Boufford 2011c) and are not repeated here.

TAXONOMY AND FORMAT

The taxonomy and nomenclature adopted for this work primarily follow that of draft treatments for the Flora of North America project and checklists of accepted taxa of The Flora of North America Expertise Network, except that families, genera, and species are arranged alphabetically. The families and their circumscription do not necessarily reflect current views on relationships or composition. The Angiosperm Phylogeny Website (Stevens 2001 onwards) should be consulted for a continuously updated treatment of families and their inclusive genera. Named and unnamed hybrid taxa are placed alphabetically at the end of the genus in which they occur. Unnamed hybrids combine the names of the progenitors alphabetically by epithet. Taxa that are not native to New England are indicated by uppercase text. Unpublished names are not used, even if publication is pending.

Chromosome numbers are taken primarily from draft treatments for the Flora of North America project and from Goldblatt and Johnson (1979–).

Synonymy is provided primarily with respect to names accepted in standard manuals covering New England published from 1950 onward, including Fernald (1950), Gleason and Cronquist (1991), and Seymour (1982) and on herbarium labels in New England herbaria. Synonyms have not been provided where the distribution for the synonymized name does not include New England.

The following list (which includes excluded taxa) will aid readers in finding familiar names that have been transferred to other taxa:

Antirrhinum (in part)	=>	*Misopates*
Asperula (in part)	=>	*Galium*
CALLITRICHACEAE	=>	*PLANTAGINACEAE*
CAPRIFOLIACEAE (in part)	=>	*ADOXACEAE*
CAPRIFOLIACEAE (in part)	=>	*DIERVILLACEAE*
CAPRIFOLIACEAE (in part)	=>	*LINNAEACEAE*
Diodia (in part)	=>	*Diodella*
GENTIANACEAE (in part)	=>	*MENYANTHACEAE*
Gerardia (in part)	=>	*Agalinis*
Gerardia (in part)	=>	*Aureolaria*
HIPPURIDACEAE	=>	*PLANTAGINACEAE*
Linaria (in part)	=>	*Nuttallanthus*
LOGANIACEAE (in part)	=>	*SCROPHULARIACEAE*
Mimulus (in part)	=>	*Diplacus*
Mimulus (in part)	=>	*Erythranthe*
Nemopanthus	=>	*Ilex*
SCROPHULARIACEAE (in part)	=>	*LINDERNIACEAE*
SCROPHULARIACEAE (in part)	=>	*MAZACEAE*
SCROPHULARIACEAE (in part)	=>	*OROBANCHACEAE*
SCROPHULARIACEAE (in part)	=>	*PAULOWNIACEAE*

SCROPHULARIACEAE (in part)	=>	*PHRYMACEAE*
SCROPHULARIACEAE (in part)	=>	*PLANTAGINACEAE*
Specularia	=>	*Triodanis*
Veronica (in part)	=>	*Pseudolysimachion*

The following species have been reported from our area but are excluded for the reasons noted:

CAMPANULA BONONIENSIS Linnaeus [report from Washington County, Maine, was based upon a misidentified specimen]

CAMPANULA LACTIFLORA M. von Bieberstein (*GADELLIA LACTIFLORA* (M. von Bieberstein) Schulkina) [insufficient evidence of wild occurrence -- voucher without habitat given; reported from southern Coös County, New Hampshire]

CAMPANULA LANATA Frivaldszky [no voucher of wild occurrence found; reported from Middlesex County, Massachusetts]

CASTILLEJA EXSERTA (A. Heller) T.I. Chuang & Heckard subsp. *EXSERTA* [no voucher of wild occurrence found; reported from Middlesex County, Massachusetts]

DIODIA VIRGINIANA Linnaeus var. *VIRGINIANA* [no voucher of wild occurrence found; reported from New Haven and New London counties, Connecticut]

Euphrasia × *aequalis* Callen (*E. nemorosa* (Persoon) Wettstein × *E. tetraquetra* (Brébisson) Arrondeau) [no voucher found; reported from Aroostook County, Maine]

Euphrasia suborbicularis P.D. Sell & Yeo [no voucher found; reported from Aroostook County, Maine]

GALIUM DIVARICATUM Pourret *ex* Lamarck [no voucher of certain identity and wild occurrence found; reported from Orleans County, Vermont]

Galium pilosum Aiton var. *puncticulosum* (Michaux) Torrey & A. Gray [no voucher found; reported from Connecticut]

ILEX AMBIGUA (Michaux) Torrey (*ILEX MONTANA* Torrey & A. Gray var. *MOLLIS* (A. Gray) Britton) [reported in error from Litchfield County, Connecticut, and Berkshire County, Massachusetts, based on the native *Ilex montana* Torrey & A. Gray records]

ILEX AQUIFOLIUM Linnaeus [no voucher of wild occurrence found; reported from Middlesex County, Massachusetts]

ILEX CASSINE Linnaeus [no vouchers found; reported from Grafton and Merrimack counties, New Hampshire]

KICKXIA SPURIA (Linnaeus) Dumortier [no voucher found; reported from Newport County, Rhode Island]

Limosella aquatica Linnaeus [no vouchers found; reported from Oxford and Somerset counties, Maine]

LINARIA ANGUSTISSIMA (Loiseleur-Deslongchamps) Borbás (*L. ITALICA* L.C. Treviranus) [no voucher of wild occurrence found; NEBC voucher apparently is misidentified *LINARIA VULGARIS* Miller; reported from Worcester County, Massachusetts]

LINARIA DALMATICA (Linnaeus) Miller subsp. *MACEDONICA* (Grisebach) D.A. Sutton [no voucher found; reported from Massachusetts]

LINARIA PINIFOLIA (Poiret) Thellung [no voucher of certain identity found; according to Llorenç Sáez in the draft treatment of *Linaria* for the Flora of North America project, all specimens seen in North America labeled as this species appear to be *L. MAROCCANA* J.D. Hooker and none of the Fairfield County, Connecticut, collections of Eames (#9511) are *L. PINIFOLIA* (Sáez, personal communication); reported from Fairfield County, Connecticut]

LONICERA ALPIGENA Linnaeus [no voucher of wild occurrence found; reported from Suffolk County, Massachusetts, on the grounds of the Arnold Arboretum]

LONICERA RETICULATA Rafinesque (*L. PROLIFERA* (G. Kirchner) Rehder) [no voucher of wild occurrence found; reported from Hampshire, Middlesex and Worcester counties, Massachusetts]

Lonicera villosa (Michaux) Schultes var. *fulleri* Fernald [no voucher found; reported from Norfolk County, Massachusetts]

MAZUS MIQUELII Makino (*M. REPTANS* N.E. Brown) [no vouchers of wild occurrence found; reported from Sagadahoc County, Maine, and Barnstable County, Massachusetts]

OROBANCHE MINOR Smith [no voucher of wild occurrence found; reported from Caledonia County, Vermont]

PENSTEMON BARBATUS (Cavanilles) Roth var. *BARBATUS* [no voucher of established wild occurrence found; reported from Suffolk County, Massachusetts]

RUBIA TINCTORUM Linnaeus [no voucher of established wild occurrence found; reported from Hampshire County, Massachusetts]

SCABIOSA ATROPURPUREA Linnaeus [no voucher found; reported from Waldo County, Maine]

SCABIOSA COLUMBARIA Linnaeus [no voucher of wild occurrence found; reported from Suffolk County, Massachusetts]

SUCCISA PRATENSIS Moench [no voucher of wild occurrence found; reported from Essex County, Massachusetts]

Utricularia striata Leconte *ex* Torrey (*U. fibrosa* misapplied) [no vouchers found; reported from Hartford County, Connecticut, and Barnstable County, Massachusetts]

VERONICA HEDERIFOLIA Linnaeus [no voucher of wild occurrence found; reported from Connecticut, and Newport County, Rhode Island]

VERONICA POLITA Fries [no voucher of wild occurrence found; reported from New Haven County, Connecticut, and Franklin and Oxford counties, Maine]

ANGIOSPERMAE (MAGNOLIOPHYTA) – ANGIOSPERMS

ACANTHACEAE

Justicia americana (Linnaeus) Vahl—(Figure 2). $2n = 26$. Margins or shallow beds of streams.

ADOXACEAE

SAMBUCUS EBULUS Linnaeus—Danewort (Figure 2). $2n = 36$. Roadsides. From Eurasia, northern Africa.

SAMBUCUS NIGRA Linnaeus subsp. *NIGRA*—European Elder (Figure 2). $2n = 36$. Waste ground. From Eurasia, northern Africa.

Sambucus nigra Linnaeus subsp. *canadensis* (Linnaeus) Bolli—Common Elder (Figure 2). $2n = 36$. Swamps, wet woods, damp roadsides, moist soil. [*S. canadensis* Linnaeus]

Sambucus racemosa Linnaeus subsp. *pubens* (Michaux) Hultén—Red-berried Elder (Figure 2). $2n = 36, 38$. Rich woods, openings, often rocky. [*S. pubens* Michaux]

Viburnum acerifolium Linnaeus—Maple-leaved Viburnum (Figure 2). $2n = 18$. Open woods.

Viburnum dentatum Linnaeus var. *dentatum*—Southern Arrow-wood (Figure 2). $2n = 36, 72$. Damp thickets, railroad ditches. [*V. dentatum* var. *deamii* (Rehder) Fernald); *V. dentatum* var. *scabrellum* Torrey & A. Gray; *V. dentatum* var. *pubescens* Aiton; *V. pubescens* (Aiton) Pursh]

Viburnum dentatum Linnaeus var. *venosum* (Britton) Gleason—(Figure 2). $2n = ?$ Sandy soil, brackish marshes.

VIBURNUM DILATATUM Thunberg—Linden Viburnum (Figure 2). $2n = 18$. Woods. From eastern Asia.

Viburnum edule (Michaux) Rafinesque—Squashberry (Figure 3). $2n = 18$. Woods, thickets, clearings by shores.

VIBURNUM LANTANA Linnaeus—Wayfaring-tree (Figure 3). $2n = 18$. Waste places, roadsides. From Eurasia, northern Africa.

Viburnum lantanoides Michaux—Hobblebush (Figure 3). $2n = 18$. Rich, moist woods, cool ravines, stream margins. [*V. alnifolium* misapplied]

Viburnum lentago Linnaeus—Nannyberry (Figure 3). $2n = 18$. Moist thickets, woodland margins, streambanks, roadsides.

Viburnum nudum Linnaeus var. *nudum*—Possum-haw (Figure 3). $2n = 18$. Swamps.

Viburnum nudum Linnaeus var. *cassinoides* (Linnaeus) Torrey & A. Gray—Witherod (Figure 3). $2n = 18$. Thickets, clearings, swamps, woodland margins, usually in moist soil. [*V. cassinoides* Linnaeus]

VIBURNUM OPULUS Linnaeus var. *OPULUS*—Guelder-rose (Figure 3). $2n = 18$. Roadsides, shores, thickets, field margins. From Eurasia.

Viburnum opulus Linnaeus var. *americanum* Aiton—Highbush Cranberry (Figure 3). $2n = 18$. Wet thickets, shores, swamps, cool, moist woods, railroads. [*V. trilobum* Marshall]

VIBURNUM PLICATUM Thunberg—Japanese Snowball (Figure 3). $2n = 18$. Roadsides, rich or moist woods. From eastern Asia.

Viburnum prunifolium Linnaeus—Black Haw (Figure 4). $2n = 18$. Rich woods, dry limestone ledges, dry copse margins, dry, open rocky ground.

Viburnum rafinesqueanum Schultes var. *rafinesqueanum* Downy Arrow-wood (Figure 4). $2n = 36$. Waste places. Thickets, dry, rocky or open woods, dry ledges, often calcareous. [*V. pubescens* misapplied]

Viburnum recognitum Fernald—Smooth Arrow-wood (Figure 4). $2n = 36$. Damp thickets, swamps, moist woods. [*V. dentatum* Linnaeus var. *lucidum* Aiton]

VIBURNUM SETIGERUM Hance—Tea Viburnum (Figure 4). $2n = 18$. Fields, woodland margins, hillsides. From eastern Asia.

VIBURNUM SIEBOLDII Miquel—(Figure 4). $2n = 16$. Woodland margins, disturbed woodlands, moist deciduous woods, field margins, waste places, cemeteries. From Japan.

AQUIFOLIACEAE

ILEX CRENATA Thunberg—Japanese Holly (Figure 4). $2n = 34$. Dry, oak woodland margins, thickets. From eastern Asia.

Ilex glabra (Linnaeus) A. Gray—Inkberry (Figure 4). $2n = ?$ Swamps, wet woods, low sandy or peaty soil.

Ilex laevigata (Pursh) A. Gray—Smooth Winterberry (Figure 4). $2n = ?$ Swamps, wet woods, thickets.

Ilex montana Torrey & A. Gray—(Figure 4). $2n = ?$ Rich wooded slopes and mountainsides.

Ilex mucronata (Linnaeus) M. Powell, Savolainen, S. Andrews—Mountain-holly (Figure 5). $2n = 40$. Swamps, bogs, damp thickets, cool, damp woods. [*Nemopanthus mucronatus* (Linnaeus) Trelease *ex* Loesener]

Ilex opaca Aiton var. *opaca*—American Holly (Figure 5). $2n = 36$. Moist, often sandy, woods, dune hollows, swamps and swamp margins.

Ilex verticillata (Linnaeus) A. Gray—Common Winterberry (Figure 5). $2n = 36$. Swamps, damp thickets, wet woods, pond margins. [*I. verticillata* var. *cyclophylla* B.L. Robinson; *I. verticillata* var. *fastigiata* (E.P. Bicknell) Fernald; *I. verticillata* var. *padifolia* (Willdenow) Torrey & A. Gray *ex* S. Watson; *I. verticillata* var. *tenuifolia* (Torrey) S. Watson]

BIGNONIACEAE

CAMPSIS RADICANS (Linnaeus) Bureau—Trumpet-creeper (Figure 5). $2n = 40$. Fields, woods, thickets, waste places, roadsides, railroad right-of-ways. From farther south and west.

— *Campsis* hybrid —

CAMPSIS × *TAGLIABUANA* (Visiani) Rehder—(Figure 5). [*C. GRANDIFLORA* (Thunberg) K. Schumann × *C. RADICANS* (Linnaeus) Bureau]

CATALPA BIGNONIODES Walter—Southern Catalpa (Figure 5). $2n = 40$. Roadsides, waste places, streambanks. From farther south.

CATALPA OVATA G. Don—Chinese Catalpa (Figure 5). $2n = 40$. Roadsides, railroads, waste places, streambanks. From China.

CATALPA SPECIOSA Teas—Northern Catalpa (Figure 5). $2n = 40$. Roadsides, railroads, waste places, moist woods, streambanks. From farther south and west.

CAMPANULACEAE

Campanula aparinoides Pursh—Marsh Bellflower (Figure 5). $2n = 34, 68$. Swamps, shores, meadows. [*C. aparinoides* var. *grandiflora* Holzinger; *C. uliginosa* Rydberg]

CAMPANULA CARPATICA Jacquin—Tussock Bellflower (Figure 6). $2n = 34$. Fields. From eastern Europe.

CAMPANULA DIVARICATA Michaux—Southern Harebell (Figure 6). $2n = 34$. Railroad ballast. From farther south.

CAMPANULA GLOMERATA Linnaeus—Dane's-blood (Figure 6). $2n$ = 30, 34, (90). Fields, roadsides. From Eurasia.

CAMPANULA LATIFOLIA Linnaeus—Giant Bellflower (Figure 6). $2n$ = 34. Roadsides, waste areas. From Eurasia.

CAMPANULA MEDIUM Linnaeus—Canterbury-bells (Figure 6). $2n$ = 32, 34. Waste places. From southern Europe.

CAMPANULA PATULA Linnaeus—(Figure 6). $2n$ = 20, 40. Waste places, fields, roadsides, riverbanks. From eastern Asia.

CAMPANULA PERSICIFOLIA Linnaeus—(Figure 6). $2n$ = 16. Wooded banks, cedar groves on high bluffs, shady ditches, wet meadows, roadsides, waste places. From Eurasia. [*C. PERSICIFOLIA* var. *ALBA* Hortulanorum]

CAMPANULA PUNCTATA Lamarck—(Figure 6). $2n$ = 34. Roadsides. From eastern Asia.

CAMPANULA RAPUNCULOIDES Linnaeus—Creeping Bellflower (Figure 6). $2n$ = 68, 102. Roadsides, thickets, waste places. From Eurasia. [*C. RAPUNCULOIDES* var. *UCRANICA* (Besser) K. Koch]

Campanula rotundifolia Linnaeus—Harebell (Figure 7). $2n$ = 34, 68, 102. Ledges, rocky slopes, gravelly or rocky shores, meadows, fields, often in calcareous soil.

CAMPANULA TRACHELIUM Linnaeus—Bats-in-the-belfry (Figure 7). $2n$ = 34. Waste places. From Eurasia, northern Africa.

JASIONE MONTANA Linnaeus—Sheep's-bit (Figure 7). $2n$ = 12. Roadsides, sandy banks, fields, waste places, often in sandy soil. From Eurasia.

Lobelia cardinalis Linnaeus—Cardinal-flower (Figure 7). $2n$ = 14. Along streams, other freshwater shores, meadows, swamps.

Lobelia dortmanna Linnaeus—Water Lobelia (Figure 7). $2n$ = 14. Sandy or gravelly pond shores in shallow water.

Lobelia inflata Linnaeus—Indian Tobacco (Figure 7). $2n$ = 14. Fields, clearings, open woods, roadsides, waste places.

Lobelia kalmii Linnaeus—Brook Lobelia (Figure 7). $2n$ = 14. Shores, bogs, *Thuja* swamps, in calcareous soil.

Lobelia siphilitica Linnaeus var. *siphilitica*—Great Blue Lobelia (Figure 7). $2n$ = 14. Wet spots, often in calcareous soil.

Lobelia spicata Lamarck—Pale-spiked Lobelia (Figure 7). $2n$ = 14. Rich meadows, moist fields, woodland trails and openings. [*L. spicata* var. *campanulata* McVaugh; *L. spicata* var. *hirtella* A. Gray]

Triodanis perfoliata (Linnaeus) Nieuwland subsp. *perfoliata*—Venus's Looking-glass (Figure 8). $2n = 60$. Woods, ledges, sandy soil, sterile, often disturbed, open ground. [*Specularia perfoliata* (Linnaeus) A. de Candolle]

CAPRIFOLIACEAE

Lonicera canadensis Bartram & W. Bartram *ex* Marshall—Fly-Honeysuckle (Figure 8). $2n = 18$. Woods, often moist or rich, woodland borders.

Lonicera dioica Linnaeus—Limber Honeysuckle (Figure 8). $2n = ?$ Open, often rocky woods, ledges, thickets, rocky banks, roadsides, fields.

LONICERA FRAGRANTISSIMA Lindley & Paxton—Sweet-Breath-of-Spring (Figure 8). $2n = ?$ Shrubby roadsides. From China.

Lonicera hirsuta Eaton—Hairy Honeysuckle (Figure 8). $2n = 18$. Wooded ledges, knolls and slopes, in calcareous soil.

LONICERA JAPONICA Thunberg—Japanese Honeysuckle (Figure 8). $2n = 18, 36$. Woodland margins, thickets, roadsides. From eastern Asia.

LONICERA KOROLKOWII Stapf—(Figure 8). $2n = ?$ Rock walls. From southwestern Asia.

LONICERA MAACKII (Ruprecht) Maximowicz—Amur Honeysuckle (Figure 8). $2n = 18$. Woods, woodland margins, fields, roadsides, thickets, waste places. From eastern Asia.

LONICERA MORROWII A. Gray—(Figure 8). $2n = 18$. Roadsides, thickets, fields, woodland margins, waste places. From eastern Asia.

Lonicera oblongifolia (Goldie) Hooker—Swamp Fly-Honeysuckle (Figure 9). $2n = 18$. Bogs, swampy thickets, wet woods. [*L. oblongifolia* var. *altissima* (Jennings) Rehder]

LONICERA PERICLYMENUM Linnaeus—European Honeysuckle (Figure 9). $2n = 18, 36, 54$. Wooded ledges near habitation, roadsides. From southern Europe, northwestern Africa.

Lonicera sempervirens Linnaeus—Trumpet Honeysuckle (Figure 9). $2n = 36$. Woods, wooded banks, thickets, shrubby ledges, roadsides.

LONICERA TATARICA Linnaeus—Tartarian Honeysuckle (Figure 9). $2n = 18$. River thickets, woodland margins, roadsides, waste places. From central Asia.

Lonicera villosa (Michaux) Schultes var. *villosa*—Mountain Fly-Honeysuckle (Figure 9). $2n = 36$. Swamps, meadows, bogs, wet woods, often in sphagnous soil. [*L. caerulea* Linnaeus var. *villosa* (Michaux) Torrey & A. Gray]

Lonicera villosa (Michaux) Schultes var. *calvescens* (Fernald & Wiegand) Fernald—(Figure 9). $2n = ?$ Swamps, meadows, bogs, wet woods, often in sphagnous soil.

Lonicera villosa (Michaux) Schultes var. *solonis* (Eaton) Fernald—(Figure 9). 2*n* = ? Swamps, meadows, bogs, wet woods, often in sphagnous soil.

Lonicera villosa (Michaux) Schultes var. *tonsa* Fernald—(Figure 9). 2*n* = ? Swamps, meadows, bogs, wet woods, often in sphagnous soil.

LONICERA XYLOSTEUM Linnaeus—European Fly-Honeysuckle (Figure 9). 2*n* = 18. Roadsides, thickets, woods, waste places. From Eurasia.

— *Lonicera* hybrids —

LONICERA × *BELLA* Zabel—(Figure 10). [*L. MORROWII* A. Gray × *L. TATARICA* Linnaeus]

LONICERA × *PURPUSII* Rehder—(Figure 10). [*L. FRAGRANTISSIMA* Lindley & Paxton × *L. STANDISHII* Carrière]

Symphoricarpos albus (Linnaeus) S.F. Blake var. *albus*—Common Snowberry (Figure 10). 2*n* = 54. Wooded, calcareous ledges.

SYMPHORICARPOS ALBUS (Linnaeus) S.F. Blake var. *LAEVIGATUS* (Fernald) S.F. Blake—(Figure 10). 2*n* = 72. Roadsides, wooded hillsides, usually near habitation. From farther west.

SYMPHORICARPOS OCCIDENTALIS Hooker—Wolfberry (Figure 10). 2*n* = 36. Waste places. From farther west.

SYMPHORICARPOS ORBICULATUS Moench—Coralberry (Figure 10). 2*n* = 18. Roadsides, fence-rows, waste places, meadows. From farther west and south.

Triosteum angustifolium Linnaeus—Yellow Horse-Gentian (Figure 10). 2*n* = ? Rocky, rich woods, thickets.

Triosteum aurantiacum E.P. Bicknell var. *aurantiacum*—Red Horse-Gentian (Figure 10). 2*n* = ? Dry, rich, rocky woods, thickets.

Triosteum perfoliatum Linnaeus—Tinker's-weed (Figure 10). 2*n* = 18. Woods, thickets, usually in rocky or thin soil.

— *Triosteum* hybrid —

Triosteum × *eamesii* (Wiegand) A. Haines—(Figure 11). [*T. angustifolium* Linnaeus × *T. aurantiacum* E.P. Bicknell var. *aurantiacum*; *T. angustifolium* Linnaeus var. *eamesii* Wiegand]

DIERVILLACEAE

Diervilla lonicera Miller—Bush-Honeysuckle (Figure 11). 2*n* = 36. Dry woods, clearings, thickets, woodland margins, rocky places.

WEIGALA FLORIBUNDA (Siebold & Zuccarini) K. Koch—Crimson Weigela (Figure 11). 2*n* = 36. Thickets, rocky roadsides. From Japan.

DIPSACACEAE

CEPHALARIA GIGANTEA (Ledebour) Bobrov—Yellow Scabious (Figure 11). 2*n* = 35, 36. Roadsides. From southwestern Asia. [*C. TATARICA* misapplied]

DIPSACUS FULLONUM Linnaeus—Fuller's Teasel (Figure 11). 2*n* = 18. Fields, roadsides, waste places. From Eurasia, northwestern Africa. [*D. SYLVESTRIS* Hudson]

DIPSACUS LACINIATUS Linnaeus—(Figure 11). 2*n* = 18. Waste places, roadsides. From Eurasia.

KNAUTIA ARVENSIS (Linnaeus) Coulter subsp. *ARVENSIS*—Bluebuttons (Figure 11). 2*n* = 20, 40. Fields, roadsides, waste places. From Eurasia.

KNAUTIA ARVENSIS (Linnaeus) Coulter subsp. *ROSEA* (Baumgarten) Soó—(Figure 11). 2*n* = ? Waste places. From Europe. [*K. DUMETORUM* Heuff]

SCABIOSA OCHROLEUCA Linnaeus—Cream Scabious (Figure 11). 2*n* = 16. Waste places, gravel pits. From Eurasia.

SUCCISELLA INFLEXA (Kluk) Beck—(Figure 12). 2*n* = 20. Low, swampy ground, river meadows. From Europe. [*SUCCISA AUSTRALIS* (Wulfen) Reichenbach]

LENTIBULARIACEAE

Pinguicula vulgaris Linnaeus subsp. *vulgaris*—Common Butterwort (Figure 12). 2*n* = 64. Wet rocks, open spots, chiefly at high altitudes.

Utricularia cornuta Michaux—(Figure 12). 2*n* = 18. Pond shores, bogs.

Utricularia geminiscapa Benjamin—(Figure 12). 2*n* = ? Ponds, pools, sluggish streams.

Utricularia gibba Linnaeus—(Figure 12). 2*n* = ? Ponds, pools, bogs. [*U. biflora* Lamarck; *U. fibrosa* Walter]

Utricularia inflata Walter—(Figure 12). 2*n* = 18, 36. Ponds.

Utricularia intermedia Hayne—(Figure 12). 2*n* = (22), 44. Ponds, pools, bogs, swamps.

Utricularia minor Linnaeus—(Figure 12). 2*n* = 36, 44. Ponds, pools, wet meadows, bogs, shores.

Utricularia purpurea Walter—(Figure 12). 2*n* = ? Ponds, sluggish streams.

Utricularia radiata Small—(Figure 13). 2*n* = ? Ponds, sluggish streams. [*U. inflata* Walter var. *minor* Chapman]

Utricularia resupinata B.D. Greene *ex* Bigelow—(Figure 13). $2n = 44$. Shores of ponds, lakes and rivers.

Utricularia subulata Linnaeus—(Figure 13). $2n = ?$ Sandy pond shores, swamps, in peat or leaf mold.

Utricularia vulgaris Linnaeus subsp. *macrorhiza* (Leconte) R.T. Clausen—(Figure 13). $2n = 36, 44$. Ponds and other quiet water. [*U. vulgaris* subsp. *vulgaris* misapplied]

LINDERNIACEAE

Lindernia dubia (Linnaeus) Pennell—(Figure 13). $2n = 18$. Muddy, sandy or gravelly shores, meadows, marshes. [*L. dubia* var. *anagallidea* (Michaux) Cooperrider; *L. dubia* var. *inundata* (Pennell) Pennell; *L. dubia* var. *riparia* (Rafinesque) Fernald; *L. anagallidea* (Michaux) Pennell; *L. pyxidaria* misapplied]

LINNAEACEAE

KOLKWITZIA AMABILIS Graebner—Beautybush (Figure 13). $2n = 32$. Riverbanks, thickets, roadsides, sandplain scrub, floodplain woods. From China.

Linnaea borealis Linnaeus var. *longiflora* Torrey—American Twinflower (Figure 13). $2n = 32$. Moist, rich, cool woods, peaty knolls, swamps. [*L. borealis* var. *americana* (J. Forbes) Rehder]

MAZACEAE

MAZUS PUMILUS (N.L. Burman) Steenis—(Figure 13). $2n = 40$. Waste places. From eastern Asia, India. [*M. JAPONICUS* (Thunberg) Kuntze]

MENYANTHACEAE

Menyanthes trifoliata Linnaeus—Buckbean (Figure 13). $2n = 54, (108)$. Bogs, pond margins, shallow water. [*M. trifoliata* var. *minor* Fernald]

Nymphoides cordata (Elliott) Fernald—(Figure 14). $2n = 36$. Ponds, lakes, slow streams.

NYMPHOIDES PELTATA (S.G. Gmelin) Kuntze—Yellow Floating-heart (Figure 14). $2n = 54, 56$. Ponds. From Eurasia. [*N. FLAVA* Druce -- illegitimate name]

OROBANCHACEAE

Agalinis decemloba (Greene) Pennell—(Figure 14). $2n = 26, 52$. Fields, woodland openings, roadsides, usually in dry, sandy soil. [*A. acuta* Pennell; *Gerardia acuta* Pennell]

Agalinis maritima (Rafinesque) Rafinesque var. *maritima*—(Figure 14). $2n = 28$. Salt marshes. [*Gerardia maritima* (Rafinesque) Rafinesque var. *maritima*]

Agalinis neoscotica (Greene) Fernald—(Figure 14). $2n = ?$ Damp sand or marshy mudflats near the sea. [*A. purpurea* (Linnaeus) Pennell var. *neoscotica* (Greene) B. Boivin; *Gerardia neoscotica* Greene]

Agalinis purpurea (Linnaeus) Pennell var. *purpurea*—(Figure 14). $2n = 28$. Swampy fields, meadows, salt marsh margins, dune hollows. [*Gerardia purpurea* Linnaeus]

Agalinis purpurea (Linnaeus) Pennell var. *parviflora* (Bentham) B. Boivin—(Figure 14). $2n = 26, 28$. Meadows, wet fields, swamps, shores, bogs, damp, open ground. [*A. paupercula* (A. Gray) Britton var. *paupercula*; *A. paupercula* var. *borealis* Pennell; *Gerardia paupercula* (A. Gray) Britton var. *paupercula*; *G. paupercula* var. *borealis* (Pennell) Deam; *G. purpurea* Linnaeus var. *parviflora* Bentham]

Agalinis tenuifolia (Vahl) Rafinesque—(Figure 14). $2n = 28$. Woodland openings, fields, thickets, roadsides, usually in dry soil. [*A. tenuifolia* var. *macrophylla* (Bentham) S.F. Blake; *A. tenuifolia* var. *parviflora* (Nuttall) Pennell; *Gerardia tenuifolia* Vahl var. *tenuifolia*; *G. tenuifolia* var. *macrophylla* Bentham; *G. tenuifolia* var. *parviflora* Nuttall]

— *Agalinis* hybrid —

Agalinis purpurea (Linnaeus) Pennell var. *parviflora* (Bentham) B. Boivin × *A. tenuifolia* (Vahl) Rafinesque—(Figure 14).

Aureolaria flava (Linnaeus) Farwell—(Figure 15). $2n = 24$. Dry, open, usually oak or oak-pine woods, roadsides. [*Gerardia flava* Linnaeus]

Aureolaria pedicularia (Linnaeus) Rafinesque *ex* Pennell—(Figure 15). $2n = 28$. Dry, open deciduous woods and clearings, roadsides, usually in sandy soil, typically parasitizing species of *Quercus*. [*A. pedicularia* var. *intercedens* Pennell; *Gerardia pedicularia* Linnaeus var. *pedicularia*; *G. pedicularia* var. *intercedens* (Pennell) Fernald]

Aureolaria virginica (Linnaeus) Pennell—Downy False Foxglove (Figure 15). $2n = 26$. Dry, open woods, usually pine and oak. [*Gerardia virginica* (Linnaeus) Britton, Sterns & Poggenburg]

Castilleja coccinea (Linnaeus) Sprengel—Scarlet Painted-cup (Figure 15). $2n = 46, 48$. Meadows, swamps.

Castilleja septentrionalis Lindley—(Figure 15). $2n = 24$. Rocky or peaty soil at high altitudes, gravelly or rocky river shores and banks.

Conopholis americana (Linnaeus) Wallroth—Squawroot (Figure 15). $2n = 40$. Rich woods, mostly under oaks, parasitic on tree roots.

Epifagus virginiana (Linnaeus) W.P.C. Barton—Beechdrops (Figure 15). $2n = ?$ Under beech trees, parasitic on their roots.

Euphrasia disjuncta Fernald & Wiegand—(Figure 15). $2n = 44$. Streambanks, damp open soil.

EUPHRASIA MICRANTHA Reichenbach—(Figure 15). $2n = 44$. Rocky summits. From Europe.

Euphrasia nemorosa (Persoon) Wallroth—(Figure 16). $2n = ?$ Fields, roadsides, woodland margins, clearings, ledges, sea bluffs. [*E. americana* Wettstein; *E. canadensis* misapplied; *E. officinalis* misapplied (in part)]

Euphrasia oakesii Wettstein—(Figure 16). $2n = ?$ Wet crevices in alpine areas. [*E. williamsii* B.L. Robinson]

Euphrasia randii B.L. Robinson—(Figure 16). $2n = ?$ Mossy banks above seashore, fields, seaside ledges, rocky turf near the sea. [*E. randii* var. *farlowii* B.L. Robinson; *E. randii* var. *reeksii* Fernald]

EUPHRASIA STRICTA J.P. Wollf *ex* J.F. Lehmann—(Figure 16). $2n = 22, 44$. Fields, roadsides, clearings. From Europe. [*E. RIGIDULA* Jordan; *E. OFFICINALIS* misapplied (in part)]

Euphrasia tetraquetra (Brébisson) Arrondeau—(Figure 16). $2n = ?$ Fields, usually dry, roadsides, grassy slopes, meadows. [*E. canadensis* Townsend]

Melampyrum lineare Desrousseaux var. *lineare*—American Cow-wheat (Figure 16). $2n = 18$. Dry woods, grassy or rocky fields and clearings, roadsides, thickets of lowbush blueberries. [*M. lineare* var. *americanum* (Michaux) Beauverd]

Melampyrum lineare Desrousseaux var. *latifolium* W.P.C. Barton—(Figure 16). $2n = ?$ Woods.

Melampyrum lineare Desrousseaux var. *pectinatum* (Pennell) Fernald—(Figure 16). $2n = ?$ Dry, sandy pine woods or oak-scrub.

ODONTITES VULGARIS Moench—Red Bartsia (Figure 16). $2n = 18, (20)$. Dry fields, roadsides, waste places. From Eurasia. [*O. SEROTINUS* misapplied; *O. VERNUS* (Bellardi) Dumortier subsp. *SEROTINUS* misapplied]

Orobanche uniflora Linnaeus—One-flowered Cancer-root (Figure 17). $2n = 18$. Damp woods and thickets, streambanks, parasitic on roots of various plants.

Pedicularis canadensis Linnaeus—Wood Betony (Figure 17). $2n = 16$. Woods, clearings, fields, meadows, roadsides, rocky shores. [*P. canadensis* var. *dobbsii* Fernald]

Pedicularis furbishiae S. Watson—Furbish's Lousewort (Figure 17). $2n = ?$ Along rivers.

Pedicularis lanceolata Michaux—Swamp Lousewort (Figure 17). $2n = 16$. Wet woods, swamps, meadows, shores and other wet ground.

RHINANTHUS MAJOR Linnaeus—(Figure 17). $2n = 22$. Wet meadows. From Europe. [*R. ALECTOROLOPHUS* (Scopoli) Pollich]

Rhinanthus minor Linnaeus subsp. *minor*—(Figure 17). $2n = 22$. Fields, roadsides, thickets, clearings. [*R. crista-galli* misapplied; *R. crista-galli* Linnaeus var. *fallax* W.D.J. Koch *ex* E.F. Linton]

Rhinanthus minor Linnaeus subsp. *groenlandicus* (Chabert) Neuman—(Figure 17). $2n = 22$. Turfy subalpine slopes. [*R. borealis* (Sterneck) Chabert]

Schwalbia americana Linnaeus—Chaffseed (Figure 17). $2n = 36$. Pine-oak woods, clearings, sandy fields.

PAULOWNIACEAE

PAULOWNIA TOMENTOSA (Thunberg) Steudel—Princess-tree (Figure 17). $2n = 40$. Waste places, roadsides, woodland margins. From China.

PEDALIACEAE

SESAMUM INDICUM Linnaeus—Sesame (Figure 18). $2n = (18), 26$. Waste places. Long cultivated, possibly from Africa or India. [*S. ORIENTALE* Linnaeus]

PHRYMACEAE

DIPLACUS BREVIPES (Bentham) G.L. Nesom—(Figure 18). $2n = 16$. Wool waste. From California and northwestern Mexico. [*MIMULUS BREVIPES* Bentham]

ERYTHRANTHE GUTTATA (de Candolle) G.L. Nesom—(Figure 18). $2n = 28$. Wet ditches, springy places, riverbanks. From farther west. [*MIMULUS GUTTATUS* de Candolle]

ERYTHRANTHE MOSCHATA (Douglas *ex* Lindley) G.L. Nesom—Muskflower (Figure 18). $2n = 32$. Wet ditches, springy places, riverbanks. From farther north and west. [*MIMULUS MOSCHATUS* Douglas *ex* Lindley]

GLOSSOSTIGMA CLEISTANTHUM W.R. Barker—(Figure 18). $2n = 50$. Sandy, silty or gravelly pond and lake shores, occasionally intertidal shores. From Australia and New Zealand.

Mimulus alatus Aiton—(Figure 18). $2n = 22$. Muddy or marshy shores, meadows, alluvial soil.

Mimulus ringens Linnaeus var. *ringens*—(Figure 18). $2n = 16, 22, 24$. Muddy shores, swamp margins, meadows, marshy shores, wet woods. [*M. ringens* var. *minthoides* (Greene) A.L. Grant]

Mimulus ringens Linnaeus var. *colpophilus* Fernald—(Figure 18). $2n = ?$ Estuaries, marshy or sandy river shores, river meadows.

Phryma leptostachya Linnaeus var. *leptostachya*—Lopseed (Figure 18). $2n = 28$. Rich, deciduous woods, usually moist.

PLANTAGINACEAE

ANTIRRHINUM MAJUS Linnaeus—Common Snapdragon (Figure 19). $2n = 16, 24, 32$. Waste places. From the Mediterranean.

Callitriche hermaphroditica Linnaeus—(Figure 19). $2n = 6$. Lakes, ponds, often calcareous.

Callitriche heterophylla Pursh var. *heterophylla*—(Figure 19). $2n = (10), 20$. Ponds, pools, lakes, quiet water of streams, intertidal mudflats. [*C. anceps* Fernald]

Callitriche palustris Linnaeus—(Figure 19). $2n = (10), 20$. Ponds, pools, lakes, quiet water of streams, springs. [*C. verna* Linnaeus]

CALLITRICHE STAGNALIS Scopoli—Common Water-starwort (Figure 19). $2n = 10, (18), (20)$. Streams, pools, ponds, lakes, springs. From Eurasia, northwestern Africa.

Callitriche terrestris Rafinesque—(Figure 19). $2n = 10$. Woodland roads, paths and margins, in damp, shady soil. [*C. deflexa* A. Braun *ex* Hegelmaier var. *austini* (Engelmann *ex* A. Gray) Hegelmaier]

CHAENORHINUM MINUS (Linnaeus) Lange subsp. *MINUS*—(Figure 19). $2n = 14, 28$. Waste places, roadsides, railroads. From Eurasia.

Chelone glabra Linnaeus—White Turtlehead (Figure 19). $2n = 28$. Swamps, wet ditches, riverbanks, wet woods, thickets, and meadows, pond and lake shores, marshes. [*C. glabra* var. *dilatata* Fernald & Wiegand; *C. glabra* var. *elatior* Rafinesque]

CHELONE LYONII Pursh—Pink Turtlehead (Figure 19). $2n = 28$. Swamps, stream banks, marsh margins. From farther south.

CHELONE OBLIQUA Linnaeus var. *OBLIQUA*—Red Turtlehead (Figure 20). $2n = 56, 84$. Wet woods. From farther south.

Collinsia parviflora Lindley—(Figure 20). $2n = 14, 28$. Base of slate cliff in dry ground.

CYMBALARIA MURALIS G. Gaertner, B. Meyer, & Scherbius—Kenilworth Ivy (Figure 20). $2n = 14$. Stone walls, waste places, dry, rocky ground, railroads, river shores. From Europe.

DIGITALIS GRANDIFLORA Miller—Yellow Foxglove (Figure 20). $2n = 56$. Fields, waste places, roadsides, open woods, thickets, woodland margins. From Eurasia. [*D. AMBIGUA* Murray]

DIGITALIS LAEVIGATA Waldstein & Kitaibel—(Figure 20). $2n =$ ca. 56. Woodland margins. From Balkan Europe.

DIGITALIS LANATA Ehrhart—Grecian Foxglove (Figure 20). $2n = 56$. Fields, roadsides, waste places. From Eurasia.

DIGITALIS LUTEA Linnaeus—Straw Foxglove (Figure 20). $2n = 56$. Roadsides, waste places. From Europe.

DIGITALIS PURPUREA Linnaeus—Common Foxglove (Figure 20). 2*n* = (48), 56. Waste places, roadsides, fields, woodland margins. From Europe, northwestern Africa.

Gratiola aurea Muhlenberg—Golden Hedge-Hyssop (Figure 20). 2*n* = 28. Muddy, sandy or gravelly shores, especially acid soil of ponds and lakes, occasionally river shores and meadows.

Gratiola neglecta Torrey—(Figure 21). 2*n* = 16. Muddy shores, roadside ditches, meadows, swamp and marsh margins.

GRATIOLA VIRGINIANA Linnaeus var. *VIRGINIANA*—(Figure 21). 2*n* = 16. Muddy roadsides and shores. From farther south and west.

Hippuris vulgaris Linnaeus—Mare's-tail (Figure 21). 2*n* = 32. Shallow, quiet waters of rivers, freshwater pools, ponds and lakes.

KICKXIA ELATINE (Linnaeus) Dumortier—(Figure 21). 2*n* = 36. Waste places, in dry, open clay. From Eurasia, northern Africa.

Limosella australis R. Brown—Welsh Mudwort (Figure 21). 2*n* = 20, 48. Tidal mud flats, occasionally muddy or sandy inland shores. [*L. subulata* E. Ives]

LINARIA BIPARTITA (Ventenat) Willdenow—(Figure 21). 2*n* = 12. Dry fields, waste places, roadsides. From Morocco. [Note: The name *L. BIPARTITA* has been misapplied to *L. INCARNATA* (Ventenat) Sprengel of southwestern Europe and Morocco.]

LINARIA DALMATICA (Linnaeus) Miller subsp. *DALMATICA*—Balkan Toadflax (Figure 21). 2*n* = 12. Waste places, roadsides, railroads, dunes, fields. From Balkan Europe, southwestern Asia.

LINARIA GENISTIFOLIA (Linnaeus) Miller subsp. *GENISTIFOLIA*—(Figure 21). 2*n* = 12. Roadsides, railroads. From Eurasia.

LINARIA MAROCCANA J.D. Hooker—Moroccan Toadflax (Figure 21). 2*n* = 12. Fields, meadows, woodland clearings, roadsides, waste places, rocky shores. From Morocco.

LINARIA REPENS (Linnaeus) Miller—Striped Toadflax (Figure 22). 2*n* = 12. Roadsides, railroads, waste places. From western Europe.

LINARIA SPARTEA (Linnaeus) Chazelles de Prizy—Ballast Toadflax (Figure 22). 2*n* = 12. Dry fields. From southwestern Europe.

LINARIA VULGARIS Miller—Butter-and-eggs (Figure 22). 2*n* = 12. Roadsides, railroads, dry fields, waste places. From Eurasia.

Littorella americana Fernald—Shore-grass (Figure 22). 2*n* = 12. Shores and margins of lakes and ponds. [*L. uniflora* misapplied]

MISOPATES ORONTIUM (Linnaeus) Rafinesque—Weasel's-snout (Figure 22). 2*n* = 16. Waste places, moist ditches. From Eurasia, northern and eastern Africa. [*ANTIRRHINUM ORONTIUM* Linnaeus]

Nuttallanthus canadensis (Linnaeus) D.A. Sutton—Old-field Toadflax (Figure 22). 2*n* = 12. Sandy soil, waste places. [*Linaria canadensis* (Linnaeus) Dumont de Courset]

PENSTEMON CALYCOSUS Small—(Figure 22). 2*n* = 96. Sandy soil in the open, fields, roadsides. From farther south and west.

PENSTEMON CANESCENS (Britton) Britton—(Figure 22). 2*n* = 16. Hillsides. From farther south.

PENSTEMON DIGITALIS Nuttall *ex* Sims—(Figure 22). 2*n* = 96. Moist banks and fields, meadows, clearings, roadsides. From farther south and west.

PENSTEMON GRANDIFLORUS Nuttall—(Figure 23). 2*n* = 16. Fields. From farther west.

Penstemon hirsutus (Linnaeus) Willdenow—(Figure 23). 2*n* = 16. Dry fields, woods and hillsides, often in rocky soil.

PENSTEMON LAEVIGATUS Aiton—(Figure 23). 2*n* = ? Fields, woods, meadows, rocky shores, sandy banks, roadsides. From farther south.

PENSTEMON PALLIDUS Small—(Figure 23). 2*n* = 16. Sandy fields, banks, usually dry, woodland clearings, roadsides. From farther west and south.

PENSTEMON TUBAEFLORUS Nuttall—(Figure 23). 2*n* = 32. Meadows, fields, open woods, roadsides. From farther west and south. [*P. TUBAEFLORUS* var. *ACHOREUS* Fernald]

PLANTAGO ARENARIA Waldstein & Kitaibel—(Figure 23). 2*n* = 12. Waste places, roadsides, railroads, fields. From Eurasia, northern Africa. [*P. INDICA* Linnaeus; *P. PSYLLIUM* Linnaeus -- rejected name]

Plantago aristata Michaux—Bracted Plantain (Figure 23). 2*n* = 20. Open, sterile or sandy, disturbed soil, gravel, roadsides, fields, waste places.

PLANTAGO CORONOPUS Linnaeus—Buck's-horn Plantain (Figure 23). 2*n* = 10, 20, 30. Waste places. From Eurasia, northern Africa.

PLANTAGO LANCEOLATA Linnaeus—Ribgrass (Figure 23). 2*n* = 12, (24). Fields, roadsides, waste places. From Eurasia, northern Africa. [*P. LANCEOLATA* var. *SPHAEROSTACHYA* Mertens & W.D.J. Koch; *P. ALTISSIMA* misapplied]

PLANTAGO MAJOR Linnaeus—Common Plantain (Figure 24). 2*n* = 12, (24), (32). Roadsides, waste places, disturbed soil. From Eurasia. [*P. MAJOR* var. *PILGERI* Domin; *P. MAJOR* var. *SCOPULORUM* Fries & Broberg; *P. INTERMEDIA* Gilibert]

Plantago maritima Linnaeus—Seaside plantain (Figure 24). 2*n* = 12, (24). Salt marshes, beaches, coastal rocks. [*P. maritima* var. *juncoides* (Lamarck) A. Gray; *P. juncoides* Lamarck var. *decipiens* (Barnéoud) Fernald; *P. juncoides* var. *glauca* (Hornemann) Fernald; *P. oliganthos* Roemer & Schultes var. *oliganthos*; *P. oliganthos* var. *fallax* Fernald]

PLANTAGO MEDIA Linnaeus—Hoary Plantain (Figure 24). 2*n* = 12, 24. Fields, roadsides, waste places. From Eurasia.

PLANTAGO PATAGONICA Jacquin—(Figure 24). $2n = 20$. Railroads, fields, waste places. From farther west, southern South America. [*P. PURSHII* Roemer & Schultes]

Plantago pusilla Nuttall—(Figure 24). $2n = 12$. Dry, sandy roadsides, fields, railroads and clearings, dry ledges.

Plantago rugelii Linnaeus—(Figure 24). $2n = 24$. Roadsides, wood roads, waste places, meadows, shores, fields.

Plantago virginica Linnaeus—Pale-seed Plantain (Figure 24). $2n = 24$. Fields, ledges, open, gravelly, rocky or sandy soil, often dry.

PSEUDOLYSIMACHION SPURIUM (Linnaeus) Rauschert—Bastard Speedwell (Figure 24). $2n = ?$ Waste places, meadows. From central Asia. [*VERONICA SPURIA* Linnaeus]

VERONICA AGRESTIS Linnaeus—Field Speedwell (Figure 24). $2n = 14, 28$. Fields, roadsides, waste places. From Europe, northern Africa.

Veronica americana Schweinitz *ex* Bentham—American Brooklime (Figure 25). $2n = 36$. Springheads, brooksides, streambanks, swamps, pool margins.

VERONICA ANGALLIS-AQUATICA Linnaeus—Water Speedwell (Figure 25). $2n = (18), 36$. Wet ditches, springs, brooksides, shores, swamps. From Eurasia, Africa, southern and western South America. [*V. CATENATA* misapplied; *V. COMOSA* misapplied]

VERONICA ARVENSIS Linnaeus—Corn Speedwell (Figure 25). $2n = 16$. Open, waste places, ledges, fields, open woods, roadsides. From Eurasia, northern Africa.

VERONICA BECCABUNGA Linnaeus—European Brooklime (Figure 25). $2n = 18, 36$. Wet ditches, freshwater shores, moist woods. From Eurasia, northern Africa.

VERONICA CHAMAEDRYS Linnaeus—Germander Speedwell (Figure 25). $2n = (16), 32$. Fields, thickets, woodland margins, roadsides, waste places. From Eurasia.

VERONICA FILIFORMIS Smith—Creeping Speedwell (Figure 25). $2n = 14$. Waste places. From the Caucasus.

VERONICA LONGIFOLIA Linnaeus—Garden Speedwell (Figure 25). $2n = 34, (36), (64), 68$. Roadsides, thickets, fields, waste places. From Eurasia.

Veronica officinalis Linnaeus var. *officinalis*—Common Speedwell (Figure 25). $2n = 18, (34), 36$. Open woods, clearings, fields, hills, usually in dry soil.

Veronica peregrina Linnaeus—Purslane Speedwell (Figure 25). $2n = 52$. Waste places, roadsides, fields, meadows, in the open, usually in moist soil. [*V. peregrina* var. *xalapensis* (Kunth) Pennell]

VERONICA PERSICA Poiret—Bird's-eye Speedwell (Figure 26). $2n = 28$. Waste places, roadsides. [*V. TOURNEFORTII* misapplied]

Veronica scutellata Linnaeus—Marsh Speedwell (Figure 26). $2n = 18$. Swamps, meadows, shores, other wet places.

Veronica serpyllifolia Linnaeus—Thyme-leaved Speedwell (Figure 26). $2n = 14, (28)$. Fields, meadows, roadsides, damp, open woods, clearings, springy places, brooksides, shores, swamps. Native in northern New England, naturalized elsewhere in New England (from Eurasia, northwestern Africa). [*V. serpyllifolia* var. *humifusa* (Dickson) Vahl; *V. tenella* Allioni]

VERONICA TEUCRIUM Linnaeus—(Figure 26). $2n = 64$. Roadsides, fields. From Eurasia. [*V. AUSTRIACA* Linnaeus subsp. *TEUCRIUM* (Linnaeus) D.A. Webb; *V. LATIFOLIA* Linnaeus -- rejected name]

VERONICA VERNA Linnaeus—Spring Speedwell (Figure 26). $2n = 16$. Railroad ballast. From Eurasia, northwestern Africa.

Veronica wormskjoldii Roemer & Schultes subsp. *wormskjoldii*—American Alpine Speedwell (Figure 26). $2n = 18, 36$. Alpine rills, ravines, moss and rocks. [*V. alpina* Linnaeus var. *unalaschcensis* Chamisso & Schlechtendal]

Veronicastrum virginicum (Linnaeus) Farwell—Culver's-root (Figure 26). $2n = 34$. Rich woods, meadows, thickets, fields, roadsides.

RUBIACEAE

ASPERULA ARVENSIS Linnaeus—Blue Woodruff (Figure 26). $2n = 22$. Waste places, roadsides, fields. From Eurasia. [*GALIUM ARVENSE* (Linnaeus) F. Hermann]

Cephalanthus occidentalis Linnaeus—Buttonbush (Figure 26). $2n = 44$. Muddy freshwater shores, swamps, bogs, marshes, pond margins.

Diodella teres (Walter) Small—Poor-joe (Figure 27). $2n = 28$. Dry, sandy soil, beaches, roadsides, waste places. [*Diodia teres* Walter]

Galium aparine Linnaeus—Cleavers (Figure 27). $2n = 64, 66$. Open, rich woods, thickets, swamps, waste places, damp ground, usually in shade.

Galium asprellum Michaux—Rough Bedstraw (Figure 27). $2n = ?$ Wet thickets and woods, meadows, low ground, roadside ditches.

Galium boreale Linnaeus—Northern Bedstraw (Figure 27). $2n = (22), 44, 66$. Fields, meadows, shores, streambanks, moist, rocky woods, roadsides. [*G. boreale* var. *hyssopifolium* (Hoffmann) de Candolle; *G. boreale* var. *intermedium* de Candolle]

Galium circaezans Michaux var. *circaezans*—Licorice Bedstraw (Figure 27). $2n = 22$. Rich, often rocky, woods, wooded ledges and talus slopes.

Galium circaezans Michaux var. *hypomalacum* Fernald—(Figure 27). $2n = ?$ Rich, often rocky, woods, wooded ledges and talus slopes.

GALIUM CONCINNUM Torrey & A. Gray—(Figure 27). 2*n* = ? Fields. From farther west.

GALIUM GLAUCUM Linnaeus—(Figure 27). 2*n* = 22, 44. Fields. From Eurasia.

Galium kamtschaticum Steller *ex* Schultes & Schultes (son)—(Figure 27). 2*n* = 22, 44. Mossy woods, brooksides, thickets, usually in mountainous areas.

Galium labradoricum (Wiegand) Wiegand—(Figure 28). 2*n* = 24. Swamps, bogs, mossy thickets, often with *Thuja occidentalis*.

Galium lanceolatum (Torrey) Torrey—(Figure 28). 2*n* = ? Dry, rich woods and thickets, often rocky.

GALIUM MOLLUGO Linnaeus—False Baby's-breath (Figure 28). 2*n* = 22, 44. Roadsides, fields, waste places. From Eurasia, northern Africa. [*G. ALBUM* Miller; *G. ERECTUM* Hudson]

Galium obtusum Bigelow subsp. *obtusum*—(Figure 28). 2*n* = 48. Meadows, marshes, low, moist woods, swampy thickets, shores. [*G. obtusum* var. *ramosum* Gleason]

GALIUM ODORATUM (Linnaeus) Scopoli—Sweet Woodruff (Figure 28). 2*n* = (22), 44, (66). Springs, meadows, woods, waste places. From Eurasia. [*ASPERULA ODORATA* Linnaeus]

Galium palustre Linnaeus—(Figure 28). 2*n* = 24, 48, 96. Meadows, swamps, low, moist woods, wet thickets, springs, streambanks, pond shores, roadside ditches.

GALIUM PARISIENSE Linnaeus—Wall Bedstraw (Figure 28). 2*n* = (22), 44, (66). Swales, ditches. From Europe.

Galium pilosum Aiton var. *pilosum*—(Figure 28). 2*n* = 22. Dry, open woods.

GALIUM SYLVATICUM Linnaeus—Scotch-mist (Figure 28). 2*n* = 22. Thicket borders, fields, roadsides, ledges, waste areas. From Europe.

Galium tinctorium Linnaeus—(Figure 29). 2*n* = ? Swamps, moist places. [*G. tinctorium* var. *floridanum* Wiegand]

GALIUM TRICORNUTUM Dandy—Corn Cleavers (Figure 29). 2*n* = (22), 44. Waste places. From Eurasia. [*G. tricorne* Stokes]

Galium trifidum Linnaeus subsp. *trifidum*—(Figure 29). 2*n* = 24. Bogs, swamps, shores, meadows, wet roadsides.

Galium trifidum Linnaeus subsp. *brevipes* (Fernald & Wiegand) Á. Löve & D. Löve—(Figure 29). 2*n* = 24. Swamps, bogs, muddy river flats, shores, roadside swales, often in calcareous soil. [*G. brevipes* Fernald & Wiegand]

Galium trifidum Linnaeus subsp. *halophilum* (Fernald & Wiegand) Puff—(Figure 29). 2*n* = ? Brackish or saline shores, salt marshes.

Galium trifidum Linnaeus subsp. *subbiflorum* (Wiegand) Puff—(Figure 29). 2*n* = ? Meadows, bogs, sandy alluvium, waste places. [*G. tinctorum* Linnaeus var. *subbiflorum* (Wiegand) Fernald]

Galium triflorum Michaux—Sweet-scented Bedstraw (Figure 29). 2*n* = 44, 66. Woods, usually moist, swamps, bogs. [*G. triflorum* var. *asprelliforme* Fernald]

GALIUM VERUM Linnaeus var. *VERUM*—Yellow Bedstraw (Figure 29). 2*n* = 22, 44, (66). Dry fields, roadsides, waste places. From Eurasia, northwestern Africa.

GALIUM VERUM Linnaeus var. *WIRTGENII* (F.W. Schultz) Nyman—(Figure 29). 2*n* = 22. Fields, meadows, roadsides, waste places. [*G. WIRTGENII* F.W. Schultz]

— *Galium* hybrid —

GALIUM × *POMERANICUM* Retzius—(Figure 30). [*G. MOLLUGO* Linnaeus × *G. VERUM* Linnaeus var. *VERUM*; *G.* × *OCHROLEUCUM* Wolf *ex* Schweigger (*pro species*)]

Houstonia caerulea Linnaeus—Bluets (Figure 30). 2*n* = 16, 32, 48. Fields, usually moist, meadows, open woods, streambanks, swamps, roadsides. [*H. caerulea* var. *faxonorum* Pease & A.H. Moore; *Hedyotis caerulea* (Linnaeus) Hooker]

Houstonia longifolia Gaertner—(Figure 30). 2*n* = 12, 24. Dry, open woods, hillsides, rocky or gravelly soil. [*Hedyotis longifolia* (Gaertner) Hooker -- illegitimate name]

Houstonia purpurea Linnaeus var. *calycosa* A. Gray—(Figure 30). 2*n* = ? Dry fields, open woods, slopes. [*H. lanceolata* (Poiret) Britton; *Hedyotis lanceolata* Poiret; *H. purpurea* (Linnaeus) Torrey & A. Gray var. *calycosa* (A. Gray) Fosberg]

Mitchella repens Linnaeus—Partridge-berry (Figure 30). 2*n* = 22. Woods.

SHERARDIA ARVENSIS Linnaeus—Field-Madder (Figure 30). 2*n* = 22. Fields, waste places. From Eurasia. [*GALIUM SHERARDIA* E.H.L. Krause]

SCROPHULARIACEAE

BUDDLEJA DAVIDII Franchet—Orange-eye Butterfly-bush (Figure 30). 2*n* = 76. Woodland margins, dry banks, roadsides, waste places. From China.

Scrophularia lanceolata Pursh—(Figure 30). 2*n* = 96. Fields, thickets, woodland margins, open woods, roadsides.

Scrophularia marilandica Linnaeus—Carpenter's-square (Figure 30). 2*n* = ca. 86. Woods, thickets, roadsides, streambanks.

SCROPHULARIA NODOSA Linnaeus—European Figwort (Figure 31). 2*n* = 36. Thickets, roadsides, waste places. From Eurasia.

VERBASCUM BLATTARIA Linnaeus—Moth Mullein (Figure 31). 2*n* = (18), 30, (32). Waste places, roadsides, fields, open woods. From Eurasia, northwestern Africa.

VERBASCUM DENSIFLORUM Bertoloni—(Figure 31). 2*n* = 30, 36. Railroads, roadsides, waste places. From Europe, the Caucasus.

VERBASCUM LYCHNITIS Linnaeus subsp. *LYCHNITIS*—White Mullein (Figure 31). 2*n* = 32, 34. Roadsides, fields, waste places, wool waste. From Eurasia.

VERBASCUM NIGRUM Linnaeus—Black Mullein (Figure 31). 2*n* = 30. Roadsides, waste places. From Eurasia.

VERBASCUM PHLOMOIDES Linnaeus—Orange Mullein (Figure 31). 2*n* = 32, 34. Roadsides, railroads, fields, waste places. From Eurasia.

VERBASCUM THAPSUS Linnaeus subsp. *THAPSUS*—Common Mullein (Figure 31). 2*n* = (30), (32), (34), 36. Roadsides, fields, rocky banks, waste places. From Eurasia.

— *Verbascum* hybrid —

VERBASCUM LYCHNITIS Linnaeus subsp. *LYCHNITIS* × *V. THAPSUS* Linnaeus subsp. *THAPSUS*—(Figure 31).

VALERIANACEAE

VALERIANA OFFICINALIS Linnaeus—Garden-Heliotrope (Figure 31). 2*n* = 14, 28, 56. Roadsides, thickets, woodland margins, waste places. From Eurasia.

Valeriana sitchensis Bongard subsp. *uliginosa* (Torrey & A. Gray) F. G. Meyer—(Figure 32). 2*n* = ? Calcareous swamps and bogs, usually with *Thuja occidentalis*. [*V. uliginosa* (Torrey & A. Gray) Rydberg *ex* Britton]

VALERIANELLA LOCUSTA (Linnaeus) Laterrade—Lamb's-lettuce (Figure 32). 2*n* = 16. Waste places, roadsides. From Eurasia, northwestern Africa. [*V. OLITORIA* (Linnaeus) Pollich]

Valerianella radiata (Linnaeus) Dufresne—(Figure 32). 2*n* = ? Riverbanks, moist fields, low ground. [*V. radiata* var. *fernaldii* Dyal]

Valerianella umbilicata (Sullivant) Alphonso Wood—(Figure 32). 2*n* = ? Damp, open places. [*V. intermedia* Dyal]

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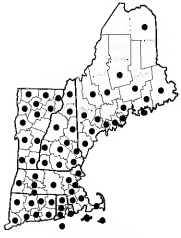
Figure 1 Key map for counties of the New England states (and Mt Desert Island, Maine; Block Island, Rhode Island; arbitrary divisions of larger Maine counties and of Coös County, New Hampshire)

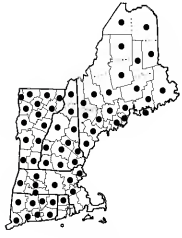
Justicia americana

SAMBUCUS EBULUS

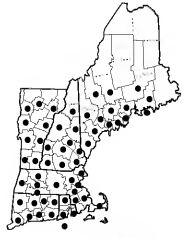
SAMBUCUS NIGRA
subsp *NIGRA*



Sambucus nigra
subsp *canadensis*



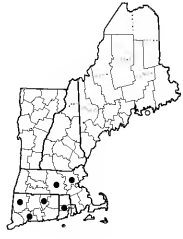
Sambucus racemosa
subsp *pubens*



Viburnum acerifolium

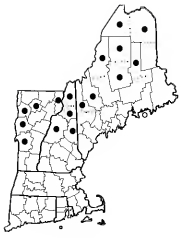
Viburnum dentatum
var. *dentatum*

Viburnum dentatum
var. *venosum*

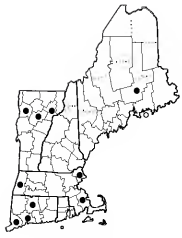


VIBURNUM DILATATUM

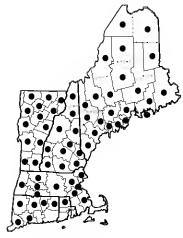
Figure 2. Distribution maps.



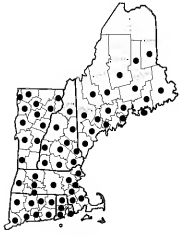
Viburnum edule



VIBURNUM LANTANA

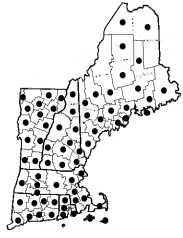


Viburnum lantanoides

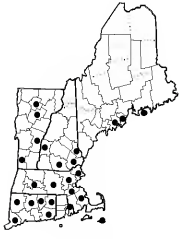


Viburnum lentago

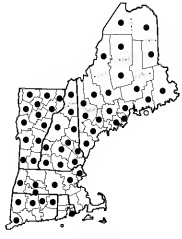
Viburnum nudum
var. *nudum*



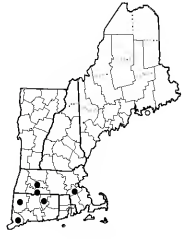
Viburnum nudum
var. *cassinoides*



VIBURNUM OPULUS
var. *OPULUS*



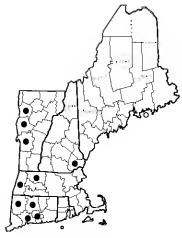
Viburnum opulus
var. *americanum*



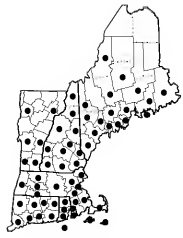
VIBURNUM PLICATUM

Figure 3. Distribution maps.

Viburnum prunifolium

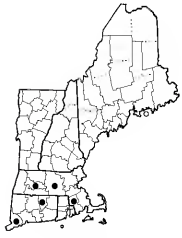


Viburnum rafinesqueanum var *rafinesqueanum*



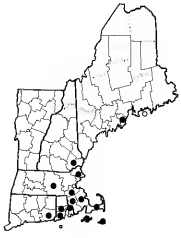
Viburnum recognitum

VIBURNUM SETIGERUM

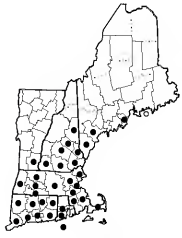


VIBURNUM SIEBOLDII

ILEX CRENATA



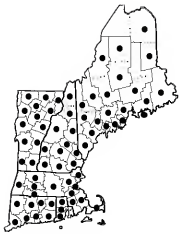
Ilex glabra



Ilex laevigata

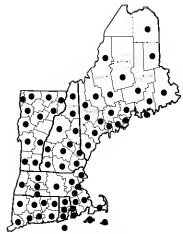
Ilex montana

Figure 4. Distribution maps.

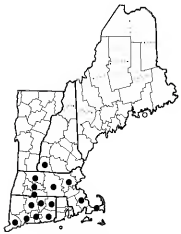


Ilex mucronata

Ilex opaca
var. *opaca*

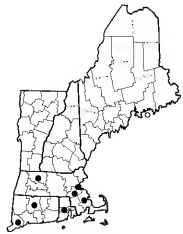


Ilex verticillata

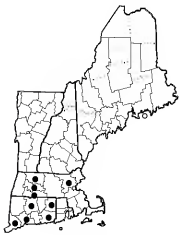


CAMPSIS RADICANS

CAMPSIS X TAGLIABUANA



CATALPA BIGNONIOIDES



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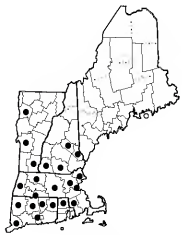
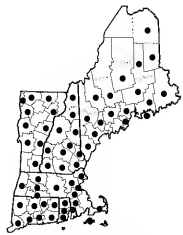
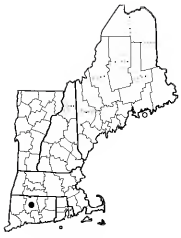


CATALPA SPECIOSA



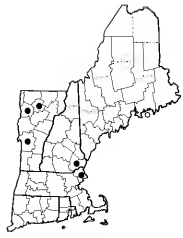
Campanula aparinoides

Figure 5. Distribution maps.



CAMPANULA CARPATICA

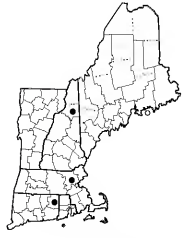
CAMPANULA DIVARICATA



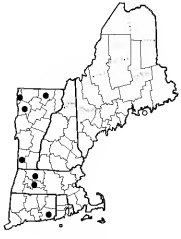
CAMPANULA GLOMERATA

CAMPANULA LATIFOLIA

CAMPANULA MEDIUM

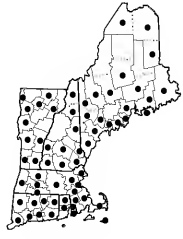


CAMPANULA PATULA



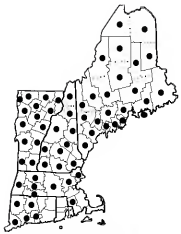
CAMPANULA PERSICIFOLIA

CAMPANULA PUNCTATA



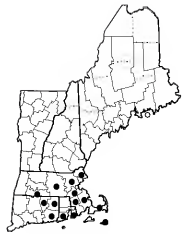
CAMPANULA RAPUNCULOIDES

Figure 6. Distribution maps.

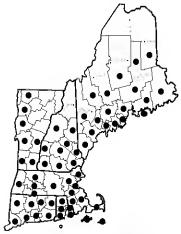


Campanula rotundifolia

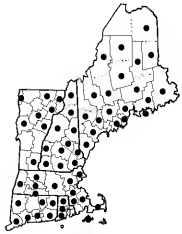
CAMPANULA TRACHELIUM



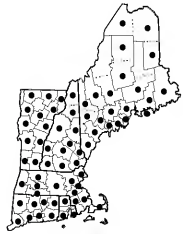
JASIONE MONTANA



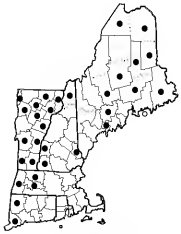
Lobelia cardinalis



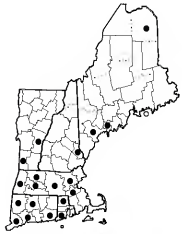
Lobelia dortmanna



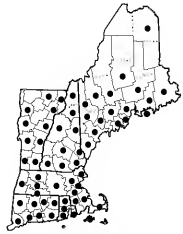
Lobelia inflata



Lobelia kalmii

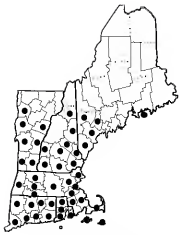


Lobelia siphilitica
var. *siphilitica*

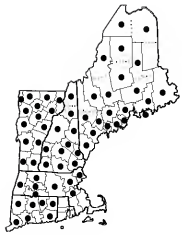


Lobelia spicata

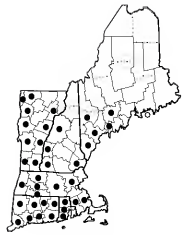
Figure 7. Distribution maps.



Triodanis perfoliata subsp. *perfoliata*



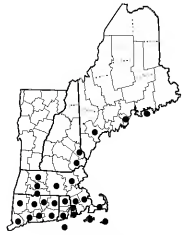
Lonicera canadensis



Lonicera dioica

LONICERA FRAGRANTISSIMA

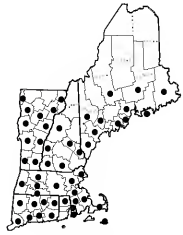
Lonicera hirsuta



LONICERA JAPONICA

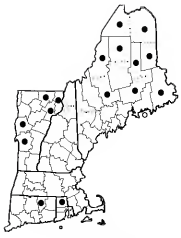
LONICERA KOROLKOWII

LONICERA MAACKII



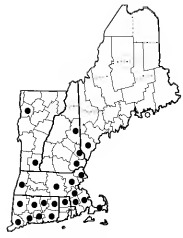
LONICERA MORROWII

Figure 8. Distribution maps.

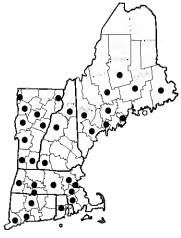


Lonicera oblongifolia

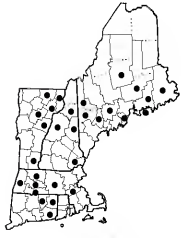
LONICERA PERICLYMENUM



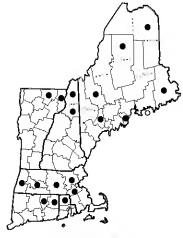
Lonicera sempervirens



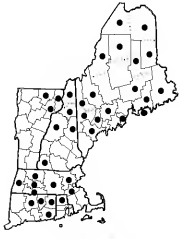
LONICERA TATARICA



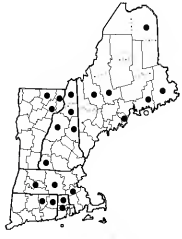
Lonicera villosa
var. *villosa*



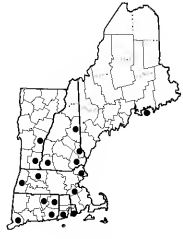
Lonicera villosa
var. *calvescens*



Lonicera villosa
var. *solonis*

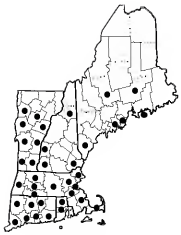


Lonicera villosa
var. *lonsa*



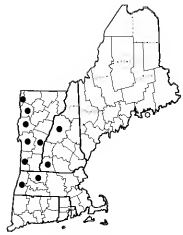
LONICERA XYLOSTEUM

Figure 9. Distribution maps.

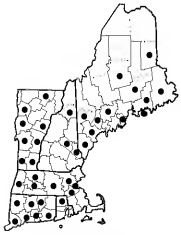


LONICERA X BELLA

LONICERA X PURPUSII

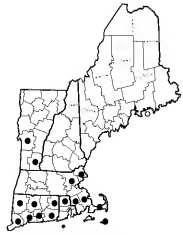


Symphoricarpos albus
var. *albus*



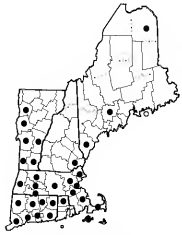
SYMPHORICARPOS ALBUS
var. *LAEVIGATUS*

SYMPHORICARPOS OCCIDENTALIS

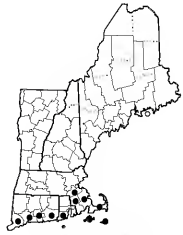


SYMPHORICARPOS ORBICULATUS

Triosteum angustifolium

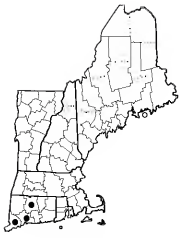


Triosteum aurantiacum
var. *aurantiacum*

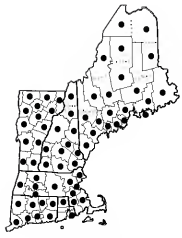


Triosteum perfoliatum

Figure 10. Distribution maps.



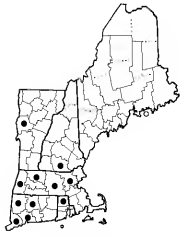
Trosteum X eamesii



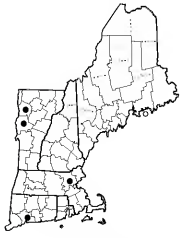
Diervilla lonicera

WEIGALA FLORIBUNDA

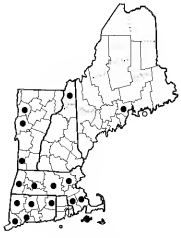
CEPHALARIA GIGANTEA



DIPSACUS FULLONUM



DIPSACUS LACINIATUS



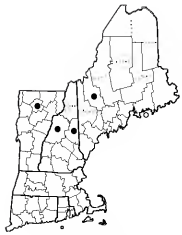
KNAUTIA ARVENSIS
subsp. *ARVENSIS*

KNAUTIA ARVENSIS
subsp. *ROSEA*

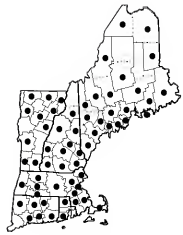
SCABIOSA OCHROLEUCA

Figure 11. Distribution maps.

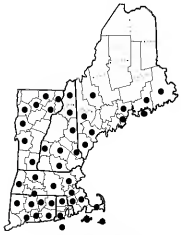
SUCCISELLA INFLEXA



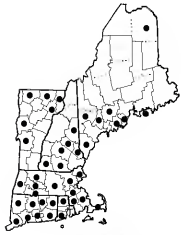
Pinguicula vulgaris subsp *vulgaris*



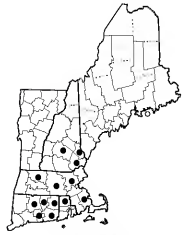
Utricularia cornuta



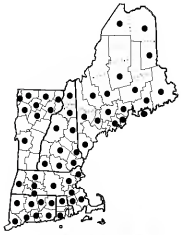
Utricularia geminiscapa



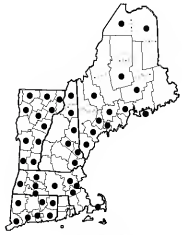
Utricularia gibba



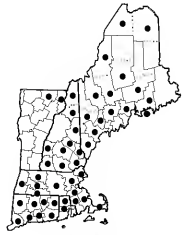
Utricularia inflata



Utricularia intermedia

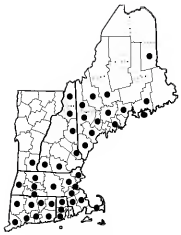


Utricularia minor

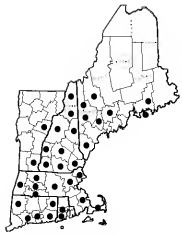


Utricularia purpurea

Figure 12. Distribution maps.

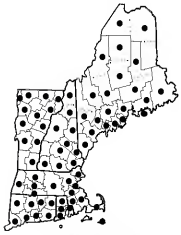


Utricularia radiata

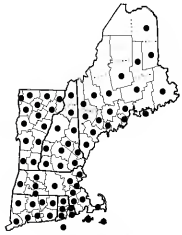


Utricularia resupinata

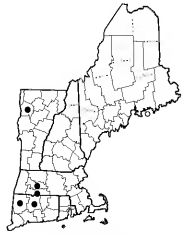
Utricularia subulata



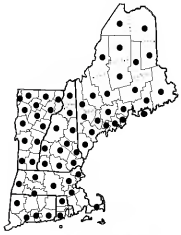
Utricularia vulgaris
subsp. *macrorhiza*



Lindernia dubia

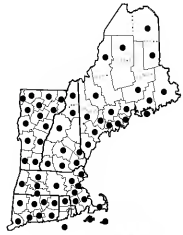


KOLKWITZIA AMABILIS



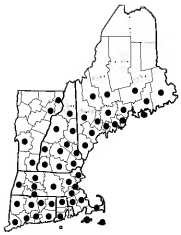
Linnaea borealis
var. *longiflora*

MAZUS PUMILUS

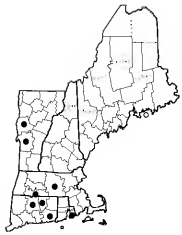


Menyanthes trifoliata

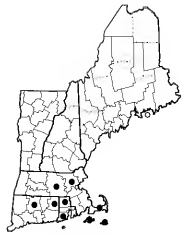
Figure 13. Distribution maps.



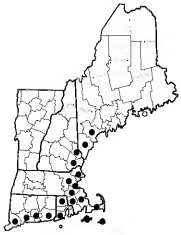
Nymphoides cordata



NYMPHOIDES PELTATA

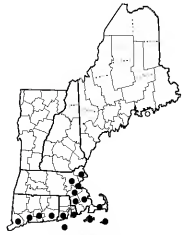


Agalinis decemloba

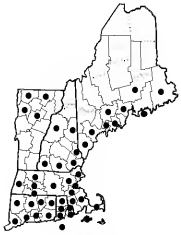


Agalinis maritima
var. *maritima*

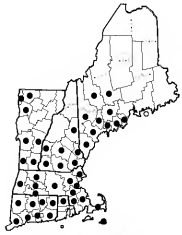
Agalinis neoscotica



Agalinis purpurea
var. *purpurea*



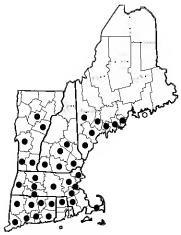
Agalinis purpurea
var. *parviflora*



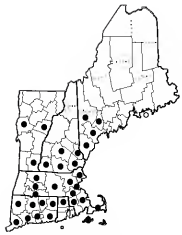
Agalinis tenuifolia

Agalinis purpurea var. *parviflora*
X *A. tenuifolia*

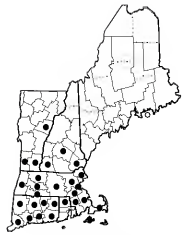
Figure 14. Distribution maps.



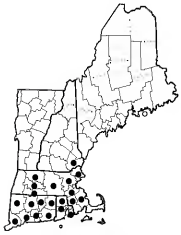
Aureolaria flava



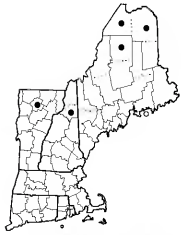
Aureolaria pedicularia



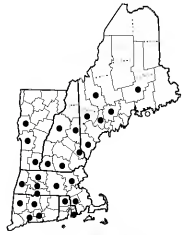
Aureolaria virginica



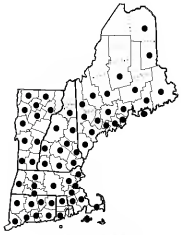
Castilleja coccinea



Castilleja septentrionalis



Conopholis americana

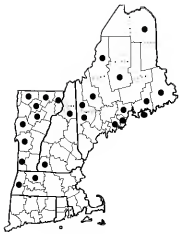


Epifagus virginiana

Euphrasia disjuncta

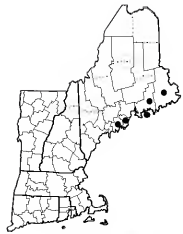
EUPHRASIA MICRANTHA

Figure 15. Distribution maps.

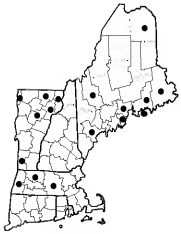


Euphrasia nemorosa

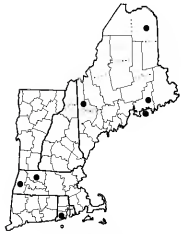
Euphrasia oakesii



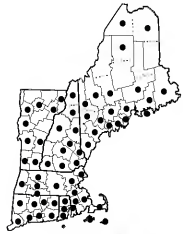
Euphrasia randii



EUPHRASIA STRICTA

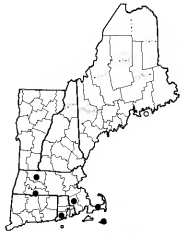


Euphrasia tetraquetra

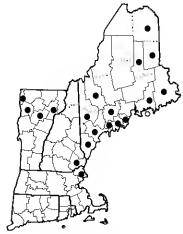


Melampyrum lineare
var. *lineare*

Melampyrum lineare
var. *latifolium*

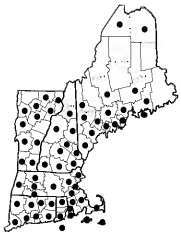


Melampyrum lineare
var. *pectinatum*

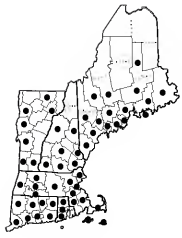


ODONTITES VULGARIS

Figure 16. Distribution maps.

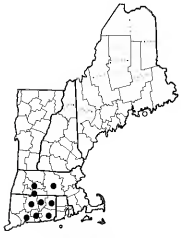


Orobanche uniflora



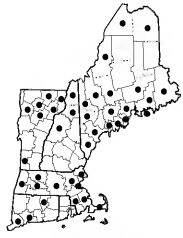
Pedicularis canadensis

Pedicularis furbishiae



Pedicularis lanceolata

RHINANTHUS MAJOR



Rhinanthus minor
subsp *minor*

Rhinanthus minor
subsp *groenlandicus*

Schwalbea americana

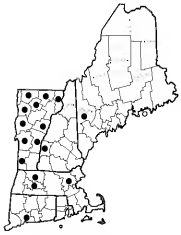
PAULOWNIA TOMENTOSA

Figure 17. Distribution maps.

SESAMUM INDICUM

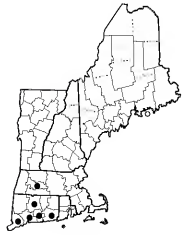
DIPLACUS BREVIPES

ERYTHRANTHE GUTTATA

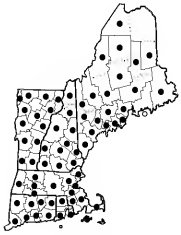


ERYTHRANTHE MOSCHATA

GLOSSOSTIGMA CLEISTANTHUM

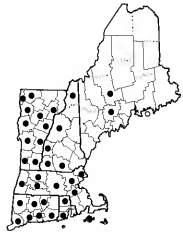


Mimulus alatus



Mimulus ringens
var. *ringens*

Mimulus ringens
var. *colpophilus*

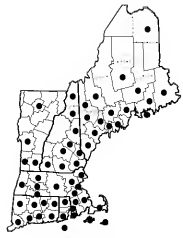


Phryma leptostachya
var. *leptostachya*

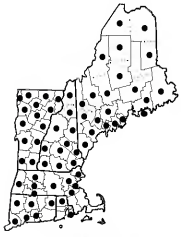
Figure 18. Distribution maps.

ANTIRRHINUM MAJUS

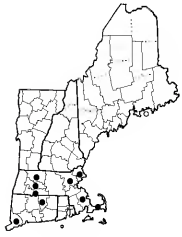
Callitriche hermaphroditica



Callitriche heterophylla var. *heterophylla*

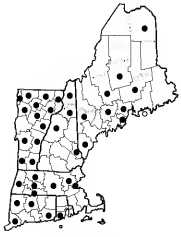


Callitriche palustris

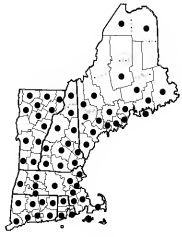


CALLITRICHE STAGNALIS

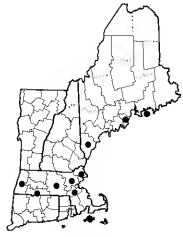
Callitriche terrestris



CHAENORHINUM MINUS subsp. *MINUS*



Chelone glabra

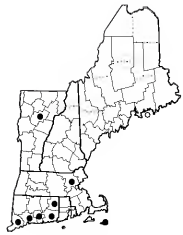


CHELONE LYONII

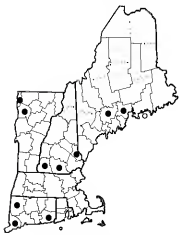
Figure 19. Distribution maps.

CHELONE OBLIQUA
var *OBLIQUA*

Collinsia parviflora



CYMBALARIA MURALIS

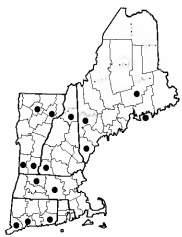


DIGITALIS GRANDIFLORA

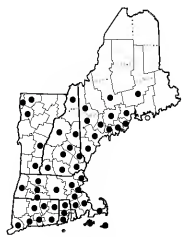
DIGITALIS LAEVIGATA

DIGITALIS LANATA

DIGITALIS LUTEA

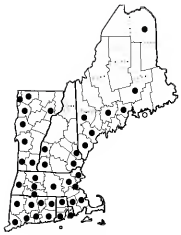


DIGITALIS PURPUREA



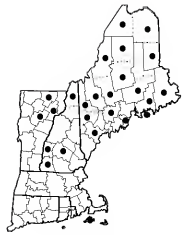
Gratiola aurea

Figure 20. Distribution maps.



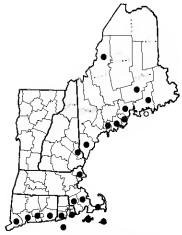
Gratiola neglecta

GRATIOLA VIRGINIANA
var. *VIRGINIANA*



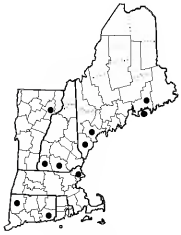
Hippuris vulgaris

KICKXIA ELATINE



Limosella australis

LINARIA BIPARTITA



LINARIA DALMATICA
subsp. *DALMATICA*

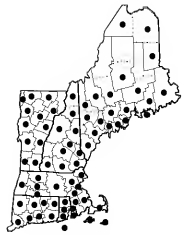
LINARIA GENISTIFOLIA
subsp. *GENISTIFOLIA*

LINARIA MAROCCANA

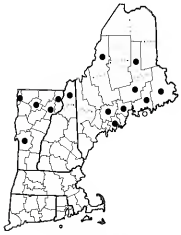
Figure 21. Distribution maps.

LINARIA REPENS

LINARIA SPARTEA

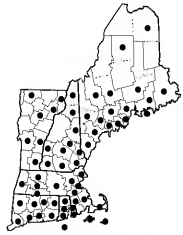


LINARIA VULGARIS

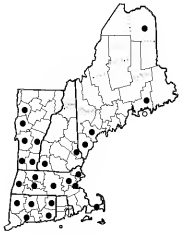


Littorella americana

MISOPATES ORONTIUM

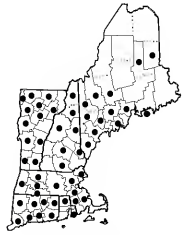


Nuttallanthus canadensis



PENSTEMON CALYCOSUS

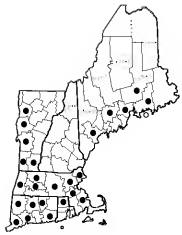
PENSTEMON CANESCENS



PENSTEMON DIGITALIS

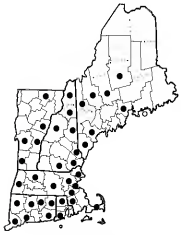
Figure 22. Distribution maps.

PENSTEMON GRANDIFLORUS

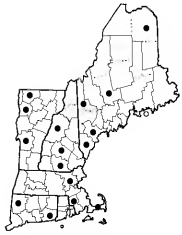


Penstemon hirsutus

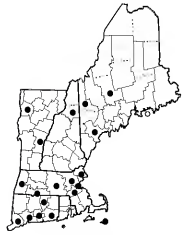
PENSTEMON LAEVIGATUS



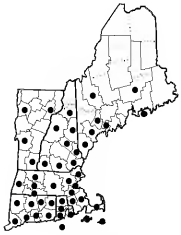
PENSTEMON PALLIDUS



PENSTEMON TUBAEFLORUS

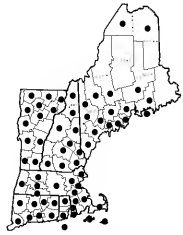


PLANTAGO ARENARIA



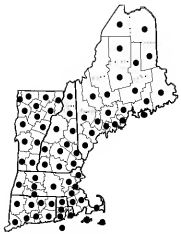
Plantago aristata

PLANTAGO CORONOPUS

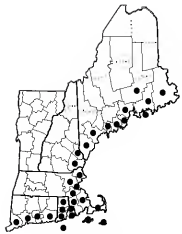


PLANTAGO LANCEOLATA

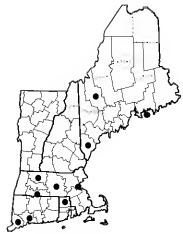
Figure 23. Distribution maps.



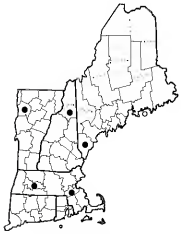
PLANTAGO MAJOR



Plantago maritima

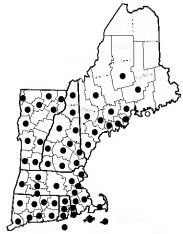


PLANTAGO MEDIA



PLANTAGO PATAGONICA

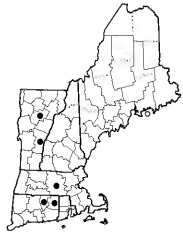
Plantago pusilla



Plantago rugelii

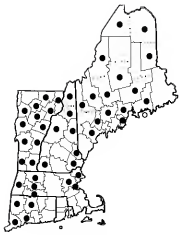
Plantago virginica

PSEUDOLYSIMACHION SPURIUM

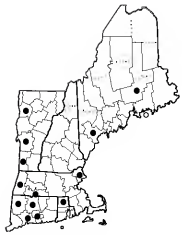


VERONICA AGRESTIS

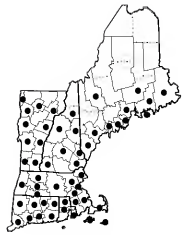
Figure 24. Distribution maps.



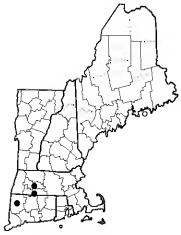
Veronica americana



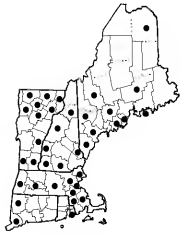
VERONICA ANAGALLIS-AQUATICA



VERONICA ARVENSIS

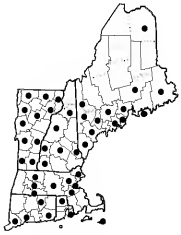


VERONICA BECCABUNGA

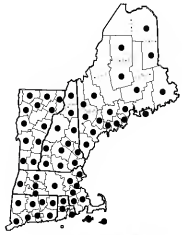


VERONICA CHAMAEDRYS

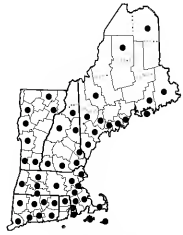
VERONICA FILIFORMIS



VERONICA LONGIFOLIA

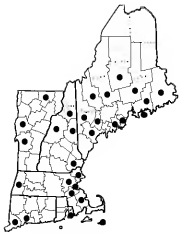


Veronica officinalis
var. *officinalis*

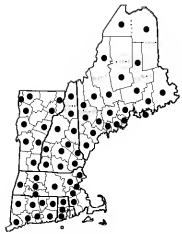


Veronica peregrina

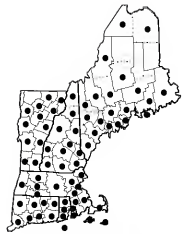
Figure 25. Distribution maps.



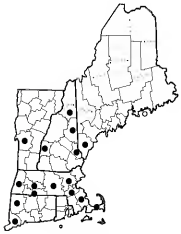
VERONICA PERSICA



Veronica scutellata



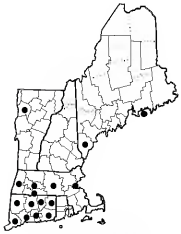
Veronica serpyllifolia



VERONICA TEUCRIUM

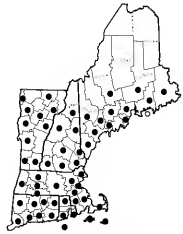
VERONICA VERNA

Veronica wormskjoldii
subsp. *wormskjoldii*



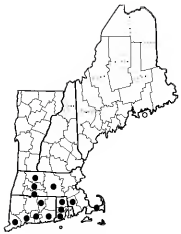
Veronicastrum virginicum

ASPERULA ARVENSIS

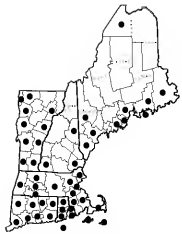


Cephalanthus occidentalis

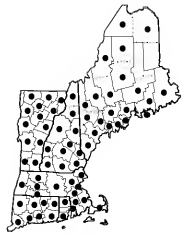
Figure 26. Distribution maps.



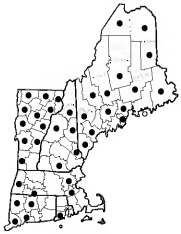
Diodella teres



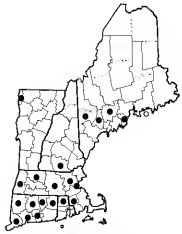
Galium aparine



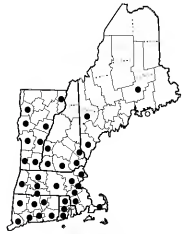
Galium asprellum



Galium boreale



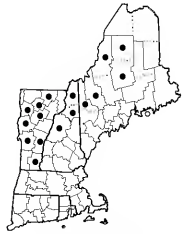
Galium circaezans
var. *circaezans*



Galium circaezans
var. *hypomalacum*

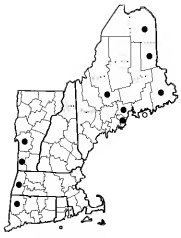
GALIUM CONCINNUM

GALIUM GLAUCUM

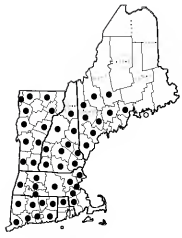


Galium kamtschaticum

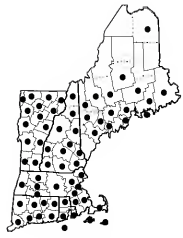
Figure 27. Distribution maps.



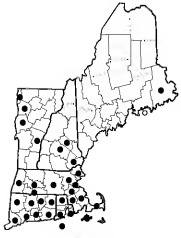
Galium labradoricum



Galium lanceolatum

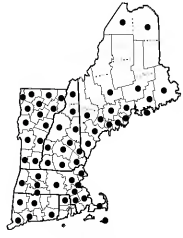


GALIUM MOLLUGO



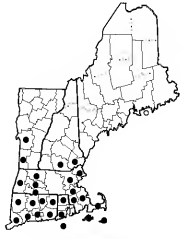
Galium obtusum
subsp. *obtusum*

GALIUM ODORATUM

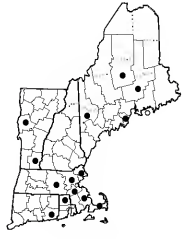


Galium palustre

GALIUM PARISIENSE

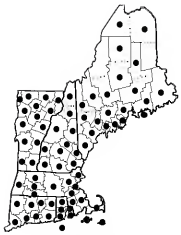


Galium pilosum
var. *pilosum*



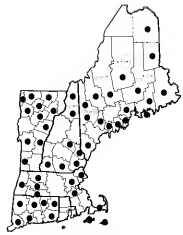
GALIUM SYLVATICUM

Figure 28. Distribution maps.

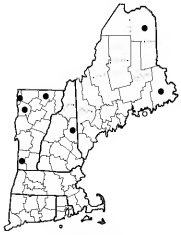


Galium tinctorum

GALIUM TRICORNUTUM

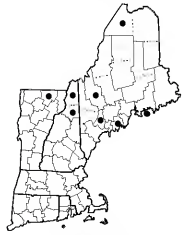


Galium trifidum
subsp. *trifidum*

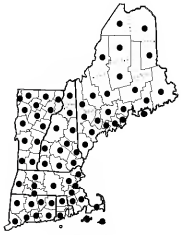


Galium trifidum
subsp. *brevipes*

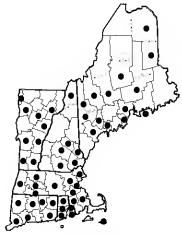
Galium trifidum
subsp. *halophilum*



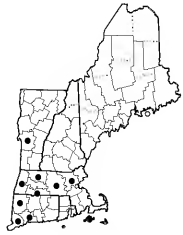
Galium trifidum
subsp. *subbiflorum*



Galium triflorum



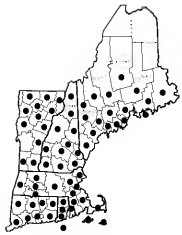
GALIUM VERUM
var. *VERUM*



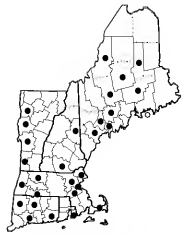
GALIUM VERUM
var. *WIRTGENII*

Figure 29. Distribution maps.

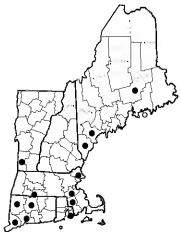
GALIUM X POMERANICUM



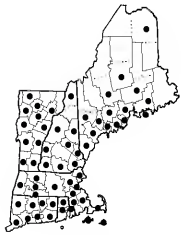
Houstonia caerulea



Houstonia longifolia



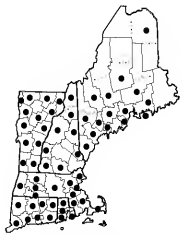
Houstonia purpurea
var. *calycosa*



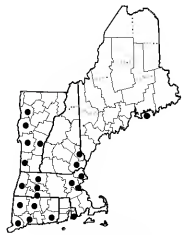
Mitchella repens

SHERARDIA ARVENSIS

BUDDLEJA DAVIDII

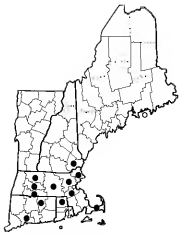


Scrophularia lanceolata

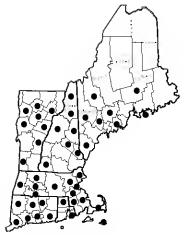


Scrophularia marilandica

Figure 30. Distribution maps.

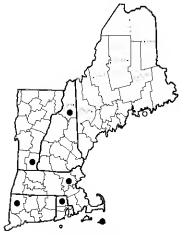


SCROPHULARIA NODOSA



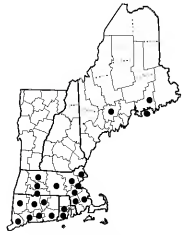
VERBSCUM BLATTARIA

VERBSCUM DENSIFLORUM

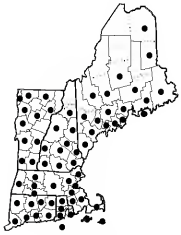


VERBSCUM LYCHNITIS
subsp. *LYCHNITIS*

VERBSCUM NIGRUM

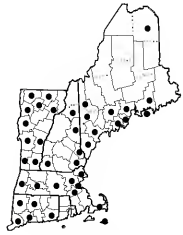


VERBSCUM PHLOMOIDES



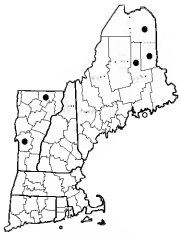
VERBSCUM THAPSUS
subsp. *THAPSUS*

VERBSCUM LYCHNITIS subsp. *LYCHNITIS*
X *V. THAPSUS* subsp. *THAPSUS*



VALERIANA OFFICINALIS

Figure 31. Distribution maps.



Valeriana sitchensis subsp. *uliginosa*

VALERIANELLA LOCUSTA

Valerianella radiata

Valerianella umbilicata

Figure 32. Distribution maps.

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NOVITATES AGROSTOLOGICAE, IV. ADDITIONAL SEGREGATES FROM *PANICUM INCERTAE SEDIS*

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ABSTRACT

In order to contribute to an updated classification of the species hitherto included in *Panicum incertae sedis*, the new genera ***Aakia*** J.R. Grande, **gen. nov**. (syn = *Panicum* sect. *Tuerckheimiana*), ***Aconisia*** J.R. Grande, **gen. nov**. (syn = *P.* [infragen. unranked] *Grandia*), and ***Osvaldoa*** J.R. Grande, **gen. nov**. (syn = *Panicum* sect. *Valida*) are described and ten new combinations in *Dallwatsonia* and *Coleataenia* are proposed. *Panicum hemitomon* is confirmed in *Hymenachne*, and consequently *Panicum* sect. *Hemitoma* is reduced to synonymy under that genus. Altogether, three new genera and 14 new combinations at the rank of species are proposed, while six infrageneric entities previously included in *Panicum* incertae sedis are formally synonymized. A lectotype is designated for *Panicum validum* Mez.

Recent systematic works dealing with the tribe Paniceae s.l. (tribe Paniceae plus tribe Paspaleae *sensu* Morrone et al. 2011) have been using the provisional taxon *Panicum* L. *incertae sedis* (i.s.) to group 158 species originally described under *Panicum* but excluded from that genus based on cladistic evidence (Aliscioni et al. 2003). Thenceforth, several new genera have been established, grouping species with more or less similar morphology, anatomy, and physiological type and with a hypothetical common ancestor including all its descendants. These studies, based on cladistic analyses using the molecular markers *ndhF*, *rpoA* and *rpoC2* and/or morphoanatomical data have been looking for a consensus between cladistic insights and previous classifications (see Morrone et al. [2011] and the subsequent Zuloaga et al. [2011] and Scataglini & Zuloaga [2013], for a review of this line of active research). Despite this, several well-defined species groups have been left behind in *Panicum* L. i.s., a clearly polyphyletic group (Gómez-Martínez 1998; Gómez-Martínez & Culham 2000; Zuloaga et al. 2000; Aliscioni et al. 2003; Morrone et al. 2011, etc.).

As a result of the comparative analysis of the general exomorphology, upper anthecium micromorphology, foliar anatomy, and geographical distribution pattern, and with the aim to further contribute to solve the present taxonomic confusion, the following new taxa previously included in *Panicum* i.s. are here described. Altogether, three new genera, 14 new combinations at the rank of species, and six new infrageneric synonyms previously included in *Panicum* i.s. are here proposed. The taxonomical novelties follow a strict alphabetical order and include only the basionyms and all its homotypic synonyms.

1. ***Aakia*** J.R. Grande, **gen. nov**. *Panicum* [infragen. unranked] *Tuerckheimiana* Hitchc., N. Amer. Fl. 17(3): 201, 210. 1915. *Panicum* sect. *Tuerckheimiana* (Hitchc.) Zuloaga, Grass Syst. Evol. [Soderstrom et al.] 296. 1988 [1987]. **Type**: *Panicum tuerckheimii* Hack.

Perennials with erect culms. Panicles more or less contracted. Spikelets lanceolate, acuminate, sparsely pilose to glabrous. Lower glume small, scalelike, nerveless. Upper glume and lower lemma pointed, 5-nerved. Lower palea reduced or absent, lower flower absent. Upper anthecium cartilaginous, papillate, pilose toward the apex.

Etymology and distribution

Aakia is a latinization of *aak*, a word commonly employed by the Maya people to refer to grasses (Bastarrachea Manzano 2011). Southern Mexico, Guatemala and Belize.

1a. Aakia tuerckheimii (Hack.) J.R. Grande, **comb. nov**. *Panicum tuerckheimii* Hack., Allg. Bot. Z. Syst. 12: 60. 1906. **TYPE: GUATEMALA**. Alta Verapaz: Cubilgütz im Hochwald, 350 m, 1903, *H. von Tuerckheim II 820* (holotype: W; isotypes: GH!, NY-232347! (fragm.), US-81303! (fragm. ex W), US-973891!, US-973890!).

Aakia belongs to subtribe Paspalinae, part of tribe Paspaleae, while *Panicum* is the type genus of true Paniceae. Endemic to Mesoamerica but phylogenetically near to the South American endemic *Anthaenantiopsis* Mez ex Pilg. (Aliscioni et al. 2003), although they apparently do not share any diagnostic morphological character. For further discussion, see under *Osvaldoa*.

2. *ACONISIA* J.R. Grande, **gen. nov**. *Panicum* [infragen. unranked] *Grandia* Hitchc., N. Amer. Fl. 17(3): 201, 209. 1915. **TYPE**: *Panicum grande* Hitchc. & Chase.

Robust and perennial gregarious grasses, producing extensively creeping or floating leafy stolons. Leaves with conspicuous lacunae in the mesophyll and superposed vascular bundles in vertical rows toward the center of the blade. Panicles with the lower primary branches whorled. Spikelets tightly disposed toward the end of terminal branches, supported by adpressed pedicels 1-2 mm long. Upper anthecium indurate with bicellular microhairs toward the apex.

Etymology and distribution

The generic name is derived from classical greek *akone*, a grindstone, which derivate verb *akonizo* produces, in passive preterite participle *akonismenos*, sharp-edged. *Aconisia* is proposed as an abbreviated and easily pronounceable form, alluding equally to the cutting borders of the leaf blades. Brazil, Panama, Trinidad & Tobago, and Venezuela.

2a. Aconisia grande (Hitchc. & Chase) J.R. Grande, **comb. nov**. *Panicum grande* Hitchc. & Chase Contr. U.S. Natl. Herb. 17: 529, f. 143. 1915. **TYPE: PANAMA**. Canal Zone: collected in the water of a swamp along the margin of Gatun Lake, 15 XII 1911, *A.S. Hitchcock 9178* (holotype: US-693329!, US-693330!, US-693331!; isotypes: F!, G!, ISC, K!, LIL!, MO-848738!, NY!, P!, SI!, W).

Aconisia is loosely similar to *Coleataenia*, with which it shares scarce prickle hairs and more or less abundant bicellular microhairs toward the apex of the upper lemma. It can be distinguished from that genus, however, by the closed sheaths (vs. widely open), wide leaf blades, panicle structure (see above), straight (vs. oblique) insertion of the spikelet into the pedicel, elliptic upper anthecium (vs. narrowly fusiform), and the anatomical characteristics cited above.

3. *COLEATAENIA* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 308. 1879.

Panicum sect. *Prionitia* Zuloaga, Grass Syst. Evol. [Soderstrom et al.] 294. 1988 [1987]. **TYPE**: *Panicum prionitis* Nees

Sorengia Zuloaga & Morrone, Taxon 59(5): 1541, 2010. **TYPE**: *Panicum agrostoides* Hitchc. & Chase, nom. illeg. superfl.

Etymology and distribution

Presumably derived from Classical Greek *colea* (sheath) and *taenia* (flat band), in allusion to the widely open leaf sheaths, which resemble a band or strip (B. Manara, pers. comm.). Tropical, subtropical and temperate America (commonly reported as "New World" in taxonomic literature).

3a. Coleataenia beyeri (Hitchc. & Ekman) J.R. Grande, **comb. nov**. *Panicum beyeri* Hitchc. & Ekman, Man. Grasses W. Ind. 165, f. 225. 1936. **TYPE: CUBA**. Oriente: E.L. Ekman 15045, 8 IX 1922 (holotype: US-1387466!; isotypus: US-1720519!).

Panicum beyeri Hitchc. & Ekman shows the characteristic leaf type of *Coleataenia*, including widely opened sheaths grading into the filiform blades, these with a conspicuous central nerve, panicles with adpressed pedicels and spikelets obliquely inserted on them, often with the first glume gaping at maturity, and with a narrowly fusiform upper anthecium. This species is very similar to *Coleataenia prionitis* (Nees) Soreng and *C. petersonii* (Hitchc. & Ekman) Soreng, which form a well-defined monophyletic unit within the genus (Hitchcock 1936; Morrone et al. 2011). *Panicum beyeri* was included neither in *Panicum* i.s. by Aliscioni et al. (2003) nor in *Coleataenia* by Soreng (2010) or Weakley et al. (2011).

4. *DALLWATSONIA* B.K. Simon, Austrobaileya 3: 678. 1992.

Etymology and distribution

Named for Michael Dallwitz, formerly of CSIRO Division of Entomology, and Leslie Watson, formerly of RSBS, Australian National University (Simon, 2013). Nine species in tropical America (commonly referred as "Neotropics" in taxonomic literature), plus two additional species in southeastern Asia (*Dallwatsonia aurita* (J. Presl ex Nees) J.R. Grande) and Australia (*D. felliana* B.K. Simon).

4a. Dallwatsonia aurita (J. Presl ex Nees) J.R. Grande, **comb. nov**. *Panicum auritum* J. Presl ex Nees, Fl. Bras. Enum. Pl. 2(1): 176-177, 1829. *Hymenachne aurita* (J. Presl ex Nees) Balansa, J. Bot. (Morot) 4: 144. 1890. **Lectotype** (designated by Veldkamp, Blumea 41: 187. 1996): **PHILIPPINE ISLANDS**. Luzon, *Haenke s.n.* (PR; isolectotypes: LE, MO-1837624!, MO-1837639!, W).

4b. Dallwatsonia bresolinii (L.B. Sm. & Wassh.) J.R. Grande, **comb. nov**. *Panicum bresolinii* L.B. Sm. & Wassh., Bradea 2: 245, f. 2 A–D. 1978. **TYPE: BRAZIL**. Santa Catarina: Florianópolis, Morro Costa da Lagaô, beira do regato, mata, 200 m, 19 IV 1967, *Klein & Bresolin 7360* (holotype: US-2536896!; isotypes: FLOR, HBR).

4c. Dallwatsonia condensata (Bertol.) J.R. Grande, **comb. nov**. *Panicum condensatum* Bertol., Opusc. Sci. 3: 408. 1819. *Hymenachne condensata* (Bertol.) Chase, J. Wash. Acad. Sci. 13: 177. 1923. **TYPE: [BRAZIL]**. Habitat in provincia di Rio de Janeiro Brasiliae, *Raddi s.n.* (holotype: BOLO; isotypes: K!, FI (3 sheets), PI, US-80598! (fragm. ex FI, PI & photo).

4d. Dallwatsonia hylaeica (Mez) J.R. Grande, **comb. nov**. *Panicum hylaeicum* Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 75. 1917. **TYPE: [BRAZIL]**. In vicinibus Santarem, Prov. Pará, VIII 1850 ["Brasilia sept., Dept. Para prope Santarem R. Spruce (Panic. n. 26)", as cited in the protologue], *R. Spruce Panicum 26* (holotype: M; isotypes: K-000309214!, P, US-80752!, (fragm. ex M & photo)).

4e. Dallwatsonia leptachne (Döll) J.R. Grande, **comb. nov**. *Panicum leptachne* Döll, Fl. Bras. 2(2): 195. 1877. **TYPE: [BRAZIL]**. Loco accuratis non indicato, *Widgren 1157* (holotype: S; isotypes: US-80737! (fragm. ex S)).

4f. Dallwatsonia longa (Hitchc. & Chase) J.R. Grande, **comb. nov**. *Panicum longum* Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 111, f. 106. 1910. **TYPE: MEXICO**. Veracruz: near Jalapa, gravelly banks, 4000 ft, 21 May 1899, *C.G. Pringle 8195* (holotype: US-354552!; isotypes: BM!, MO!, CM, M, NY!, P!, US-742435!, W). Homotypic with *Panicum pilosum* var. *macranthum* Scribn., Circ. Div. Agrostol. U.S.D.A. 19: 1. 1900. Hitchcock and Chase noted that *Panicum longum* was a "nom. nov." for *Panicum munitum* Trin. ex Steud. (1841), but since they provided a new name and new type, *P. longum* was essentially a sp. nov.

4g. Dallwatsonia pilosa (Sw.) J.R. Grande, **comb. nov**. *Panicum pilosum* Sw., Prodr. 22. 1788. **TYPE: JAMAICA**. *O.P. Swartz s.n.* (holotype: S; isotype: US-80916! (fragm. ex S)).

4h. Dallwatsonia polygonata (Schrad.) J.R. Grande, comb. nov. *Panicum polygonatum* Schrad., Mant. 2: 256. 1824. **TYPE: BRAZIL**. [Bahia]: Ad ripas fluvia Ilhéos, 1816, *Princeps Sereniss. Maximillian Neowidens s.n.* (holotype: LE; isotypes: B, BAA-1935! (fragm. ex B), US-80925! (fragm. ex LE)).

4i. Dallwatsonia stagnatilis (Hitchc. & Chase) J.R. Grande, **comb. nov**. *Panicum stagnatile* Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 528, f. 141. 1915. **TYPE: PANAMA**. Canal Zone: in water of swamp, Frijoles, 12 Oct 1911, *A.S. Hitchcock 8388* (holotype: US-693328!; isotypes: BAA! (fragm.), BM-000938691!, F!, G!, K!, LIL!, MO-853765!, MO-853766!, NY!, P!, US!, W).

4j. Dallwatsonia stevensiana (Hitchc. & Chase) J.R. Grande, **comb. nov**. *Panicum stevensianum* Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 498, f. 76. 1915. **TYPE: PUERTO RICO**. On wet sand around pool, white sand region, Campo Alegre, near Laguna del Tortugero, 25 XI 1913, *A. Chase 6616* (holotype: US-693323!; isotypes: NY-71075!, NY-71076!, US!).

Dallwatsonia was originally described as monotypic, with a single species from Australia (*D. felliana* B.K. Simon). It is here expanded, however, to include the American species left as *incertae sedis* in *Panicum* sect. *Laxa* by Aliscioni et al. (2003), plus *Panicum auritum* Presl ex Nees, a species from southeastern Asia formerly included in that section by Zuloaga et al. (1992). Phenotypic characters that may be considered diagnostic include hollow culms, secund spikelets disposed in two pararell rows along the branches of the paniele, and upper anthecium pointed, membranous to more or less indurate, with conspicuous, basally thickened prickles toward the apex, and with the apex of the palea covered by the lemma (Watson & Dallwitz 1992 onwards; Simon 2013; Zuloaga 1987; Zuloaga et al. 1992; Morrone et al. 2011). As noted in previous works (Amaya Worm 2001; Morrone et al. 2011), fusoid cells are somewhat variable in their pattern of distribution and are also present in other genera of subtribe Otachyrinae, like *Hymenachne* (e.g., *H. grumosa* (Nees) Zuloaga) and *Steinchisma* (e.g., *S. laxa* (Sw.) Zuloaga).

Although *Dallwatsonia aurita* has been considered a member of the closely related *Hymenachne*, its hollow culms are characteristic of *Dallwatsonia* (vs. filled with aerenchyma in *Hymenachne*; see Pohl & Lersten 1975). Monophyly (as well as an ambiguous holophyly) of the genus is supported by recent cladistic analyses (Morrone et al., 2011).

5. *HYMENACHNE* P. Beauv., Ess. Agrostogr., 48. 1812.

Panicum [infragen. unranked] *Hemitoma* Hitchc., N. Amer. Fl. 17(3): 200, 210. 1915. *Panicum* sect. *Hemitoma* Hitchc. & Chase ex Freckmann & Lelong, Sida 20: 163 (2002). **TYPE**: *Panicum hemitomon* Schult.

Panicum sect. *Hemitoma* is here synonymized because of the clear assignment of *P. hemitomon* to *Hymenachne*. That species, however, was included as *Panicum* i.s. by Aliscioni et al.

(2003). The diagnostic characters were noted first by Hsu (1965), who made the appropriate combination.

Etymology and distribution

From Classical Greek *hymen-* (a membrane) and *-achne* (palea; Palisot de Beauvois 1812). Tropical America, Southeastern Asia, Australia and the Pacific Islands.

Although the first species designated as the type (i.e., lectotype) of *Hymenachne* was *Hymenachne myuros* (Lam.) P. Beauv. (Pfeiffer 1873), the basionym of that name (*Panicum myuros* Lam., cited as "*Agrostis myuros* Lam." in the protologue) corresponds to *Sacciolepis myuros* (Lam.) Chase, a species not intentionally cited by Beauvois in his work, as has been shown by Niles (1925) and Panigrahi & Dubey (1986), who designated *H. monostachya* (Poir.) P. Beauv. (actually *H. amplexicaulis* (Rudge) Nees), another species' name available in the protologue, as the type of the genus.

6. ***OSVALDOA*** J.R. Grande, **gen. nov**. *Panicum* sect. *Valida* Zuloaga & Morrone, Syst. Bot. 14: 228. 1989. **TYPE**: *Panicum validum* Mez.

Caespitose, short-rhizomatous perennials. Similar to *Aakia* but differing in the linear-lanceolate leaf baldes and the first glume 3/4 the length of the spikelet.

Etymology and distribution

This genus is dedicated to Osvaldo Morrone (1957-2011), a renowned Argentinian agrostologist whose studies in the Paniceae s.l. have helped to clarify many generic boundaries. Argentina, Brazil, and Uruguay.

6a. Osvaldoa valida (Mez) J.R. Grande, **comb. nov**. *Panicum validum* Mez, Bot. Jahrb. Syst. 56 (Beibl. 125): 4. 1921. **Lectotype** (designated here): **ARGENTINA.** Entre Ríos: Concepción del Uruguay, arrollo de La China, XI 1876, *P.G. Lorentz 840* (CORD-00001751!; isolectotypes: B, BAA-00000403! (fragm. ex B) BAA-00000404! (fragm. ex B), CORD-00001750!, GOET-006793!, US-98989! [fragm. ex B]).

Based on the morphological particularities of this species, Zuloaga et al. (1989) created *Panicum* sect. *Valida* Zuloaga & Morrone. More recently, however, Aliscioni et al. (2003) have shown that both *Panicum validum* and *P. tuerckheimii* are closely related to the genus *Anthaenantiopsis*, an endemic of southern Brazil, Paraguay, and Argentina. There is not any reliable morphological synapomorphy shared by these three genera.

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I am grateful to Bruno Manara (VEN) for his expertise in classical languages and to Fernando Zuloaga (SI) for providing advice and literature.

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REDISCOVERY OF *LOBELIA BOYKINII* (CAMPANULACEAE) IN DELAWARE

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ABSTRACT

Lobelia boykinii was rediscovered in a Coastal Plain seasonal pond in Sussex Co., Delaware, after a 100 year and 19 day absence. Prior to its rediscovery, it was last collected in Sussex County on 6 July 1913. Its reappearance in the state is here recognized and aspects of the species are discussed.

Lobelia boykinii Torr. & Gray ex A. DC. (Campanulaceae) is a rhizomatous perennial and obligate wetland plant that flowers in July in Delaware. A Coastal Plain endemic, *L. boykinii* is near its northern limit of distribution in Delaware and is known from eight states in the eastern USA [New Jersey, Delaware, North Carolina, South Carolina, Georgia, Florida, Alabama, and Mississippi (NatureServe 2013)]. *Lobelia boykinii* is rare to uncommon in all eight states where it occurs (NatureServe 2013), and a Global Rank of G2G3 (imperiled to vulnerable) has been applied, based on less than 100 extant occurrences (NatureServe 2013).

Historically in Delaware, *Lobelia boykinii* has only been collected four times, first in 1893 by William Canby (Tatnall 1946; DOV) and last in 1913 by Bayard Long (Tatnall 1946; PH). All four collections were from the Ellendale area of central Sussex County. Habitats were described on collection labels as "meadows" and "ditches." The area of Ellendale is a very rural part of the state and has suffered from the negative impacts of agriculture and industrial forestry practices for many decades. Weakley (2012) describes the habitat for *L. boykinii* in the Southeast as "cypress ponds and depression meadows," and the first author has observed the species growing in seasonally flooded ponds and depressions in Georgia. Though rare due to disturbance, seasonally flooded ponds and depressions still exist in the Ellendale area and were the likely habitat types prior to the first collection in 1893.

The Ellendale area historically supported other Coastal Plain species of the Southeast that grow in seasonally flooded depression wetlands, such as *Agalinis limifolia* (Nutt.) Britt., *Muhlenbergia torreyana* (Schult.) A.S. Hitchc., *Polygala cymosa* Walt., and *Tiedemannia canbyi* (J.M. Coult. & Rose) Feist & S.R. Downie [*Oxypolis canbyi* (Coult. & Rose) Fern.]. Ellendale is the type locality for *T. canbyi*, where it was first collected by William Canby in 1867 (Tatnall 1946). Interestingly, Canby made a collection of *T. canbyi* in August of 1893 (Tatnall 1946; DOV) and of *L. boykinii* in July of the same year (Tatnall 1946; DOV). The habitats for both collections were described as "meadows, Ellendale." In South Carolina, *Lobelia boykinii* occurs at 12 sites that also support *T. canbyi* (Julie Holling, pers. comm. 2013). In Georgia, *L. boykinii* is found at two sites where *T. canbyi* is also found (Rebecca Pudner, pers.comm. 2014).

Figure 1. *Lobelia boykinii* in Sussex Co., Delaware. Photo by Ron Wilson, 25 July 2013.

In late July 2013, in Sussex Co., Delaware, while conducting a population survey of *Dichanthelium hirstii* (Hirst brothers' panic grass), a globally rare species and Candidate for Federal listing, the authors were both thrilled and stunned to find *Lobelia boykinii* (Fig. 1). Thrilled because we both knew that it had not been reported for a very long time in Delaware and was perhaps extirpated from the state, and stunned because we were about 25 miles (42 kilometers) southeast of where it was historically known, at a site that has been visited annually for 29 years! Frank Hirst (1928-2009) discovered this site in 1984, a shallow, seasonally flooded depression known as a Coastal Plain seasonal pond. The flora of Coastal Plain seasonal ponds in Delaware and on the Delmarva Peninsula are strongly influenced by fluctuating groundwater levels (McAvoy & Bowman 2002). They are typically flooded in winter and spring, draw down through the summer, and are dry by late summer or fall.

When Frank discovered this site, he found *Dichanthelium hirstii*, the grass named for him and his brother Bob (1925-1963). Prior to this discovery, *D. hirstii* was only known from southern New Jersey where the brothers first discovered it in 1959 (Swallen 1961). Due to *D. hirstii's* great rarity, population counts have been done annually since it was first found in Delaware. Since 2010, site visits and monitoring were conducted once per month, from June to November. Prior to 2010, beginning in 1984, site visits were not monthly, but usually several visits were conducted each year.

Therefore, over a 29 year period botanists have been visiting this site on a regular basis and *L. boykinii* was never observed. It is certainly possible that the species was present and flowering during one of those monitoring visits and just missed, but unlikely because the entire site was always carefully searched for new plants of *D. hirstii*. In addition to *D. hirstii* and *L. boykinii*, this site also supports many other state rare plants, such as *Boltonia asteroides* (L.) L'Her. var. *glastifolia* (Hill) Fern., *Coelorachis rugosa* (Nutt.) Nash, *Eriocaulon compressum* Lam., *Hypericum denticulatum* Walt., *Rhexia aristosa* Britt., *Rhynchospora filifolia* Gray, *R. harperi* Small, *R. inundata* (Oakes) Fern., *Sabatia difformis* (L.) Druce, *Sclerolepis uniflora* (Walt.) B.S.P., and *Xyris smalliana* Nash.

Voucher specimens. **Delaware. Sussex Co.**: 14 stems, 3 with fading flowers, in 17 inches (30 cm.) of water, stems clustered in a 30 x 20 cm. patch, in sun, this collection consists of several stems that had broken away and were floating at the water surface, growing in a seasonally flooded depression southwest of the town of Bethany Beach, with *Dichanthelium hirstii*, 25 July 2013, *W.A. McAvoy 7190 & R.M. Wilson* (DOV); "Ellendale," 6 July 1913, *Bayard Long s.n.* (PH); "ditches along railroad, Ellendale," 9 July 1908, *C.S. Williamson s.n.* (PH); "ditches along railroad, Ellendale," 20 June 1909, *C.S. Willamson s.n.* (PH); "meadows, Ellendale," 24 July 1893, *William Canby s.n.* (DOV).

It is interesting to note that *Lobelia boykinii* is an associate at 5 of the 8 locations in the USA where *Dichanthelium hirstii* is either historical or extant: New Jersey — three sites, one extant, *L. boykinii* is known from two of the sites; Delaware — one extant site, *L. boykinii* present; North Carolina — two sites, one extant, *L. boykinii* is known from both sites; and Georgia — two sites, both historical, the exact locations of the Georgia collections (Harper 1900; Thorne 1947) are not known, so *L. boykinii* may or may not have been an associate. Many years before he passed away, Frank Hirst once mentioned to the second author that he thought the pond in Delaware where he found the Hirst Brothers' panic grass "looked like a good pond for *L. boykinii*."

Lacy et al. (2001) and Royo et al. (2008) found that *Lobelia boykinii* seeds germinate in August and early September in North Carolina and then seedlings develop into rosettes, which will grow through the winter even in standing water. In April of the next season, rosettes disappear from aboveground view, to reappear later that fall. If a rosette survives its first nineteen months of life, it either flowers, or dies back to the rhizome in its second season (Lacy et al. 2001; Royo et al. 2001). Based on this life history, seeds of *L. boykinii* at the Delaware station may have germinated from a dormant seed bank in August or September of 2011 (pond dry). Rosettes that developed from seedlings would then have persisted through the winter (pond flooded), and then died back to rhizomes in April or May of 2012 (pond flooded), then reappear as rosettes again in September (pond dry). These rosettes would have lasted through the winter of 2013 (pond flooded), and then flowered in July (pond flooded). Lacey et al. (2001) cited two seed bank studies: one found no seedlings of *L. boykinii* germinating from soil cores from three sites, and another found that only freshly collected seed germinated. Lacy et al. (2001) noted that these studies suggest that seed longevity for *L. boykinii* is "short." Based on the fact that *L. boykinii* had never been observed at the Delaware location during 29 years of visitation until 2013, perhaps *L. boykinii* does seed bank and seed viability is longer than previously estimated. Additionally, Mitschunas et al. (2008) pointed out that in habitats providing irregular opportunities for seedling establishment, it may be beneficial for a species to have a long-lived seed bank in order to bridge prolonged periods without such opportunities. The flooding and draw-down cycles in the Coastal Plain seasonal ponds in Delaware are strongly influenced by local weather patterns and are therefore unpredictable, so these seasonal ponds would fit the category of a habitat that provides irregular opportunities for seedling establishment.

Lacey et al. (2001) pointed out that their observations suggest that growth of *Lobelia boykinii* is strongly influenced by standing water depth and duration. In 2012, Hurricane Sandy hit Delaware

and surrounding states on 29 October and the *L. boykinii* site in Delaware flooded with over 12 inches (30 centimeters) of water. Residual flooding from Hurricane Sandy in 2012, along with other storms in 2013, kept the pond fully flooded throughout much of the 2013 growing season. *Lobelia boykinii* in Delaware was found flowering in 17 inches of water (43 centimeters) (Fig. 1). Is flooding the mechanism that triggers flowering in *L. boykinii*? The 2012/2013 flooding of the Delaware pond was one of the deepest and longest that has been recorded during the 29 years of monitoring the site. Was *L. boykinii* dormant as an above-ground basal rosette waiting for just the right degree of flooding to flower? Conversely, a population of *L. boykinii* in New Jersey produced over 200 flowering plants on a "dry pond bottom" (David Snyder, pers. comm. 2013). Only long-term population monitoring throughout the range of the species can reveal even some of its secrets.

Lobelia boykinii is self-incompatible (Lacy et al. 2001; Royo et al. 2001) and Royo et al. (2008) found that successful fertilization of *L. boykinii* appears to be dependent on cross-pollination by insects between different genotypes within a population. According to Royo et al. (2008), small populations of *L. boykinii* have a reduced number of genotypes available for cross-pollination, which therefore limits seed production. The Delaware population of *L. boykinii* consisted of 14 stems (three stems with fading flowers) within a patch about 30 x 20 cm. in size (Fig. 1). The flowers found on three separate stems never set fruit. It is possible that this population was one genotype (clonal) and thus self-incompatible.

It will be interesting to see if *Lobelia boykinii* shows itself again in Delaware in 2014, either as a flowering plant or as a basal rosette developed from the rhizome that produced the 14 stems in 2013. According to Lacey et al. (2001), if an individual rhizome survives after flowering, it produces one to several new rosettes the following fall. The depth of flooding in the Delaware pond in 2013 was such that the pond bottom was not clear enough to tell if a rosette was present.

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NEOTYPIFICATION AND NOTES ON THE STATUS OF *CASTILLEJA TAPEINOCLADA* (OROBANCHACEAE)

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ABSTRACT

A neotype is designated for *Castilleja tapeinoclada* Loes., due to the destruction of original material in Berlin during World War II and the ambiguous nature of the original typification. Synonymy and a discussion of the status of this Guatemalan endemic species are also provided.

In 1903, Theodor Loesener of the Botanic Garden and Botanical Museum Berlin-Dahlem (B) described in his serial, Plantae Selerianae, several closely related taxa in the genus *Castilleja*, based on specimens obtained by one of the museum's field botanists, Eduard Georg Seler, in the mountainous regions of Guatemala in Central America. Loesener described *C. tapeinoclada* Loes. with two named varieties, *C. tapeinoclada* var. *subglabra* Loes. and *C. tapeinoclada* var. *hirta* Loes., as well as another closely similar species, *C. katakyptusa* Loes. Each of these entities was distinguished by minor differences in herbage pubescence, presence of leaf lobes, and/or relative measurements of the flowers and bracts. Oddly, Loesener designated type collections for the two varietal names, var. *subglaber* (*Seler 2357*) and var. *hirta*, (*Seler 2933*), but made no such designation for *C. tapeinoclada* itself. Presumably, Loesener intended the first-mentioned form, var. *subglaber*, to serve as the equivalent of the species' nominate form, but this is conjectural and the typification of the species names remains ambiguous. *Castilleja katakyptusa* was described as monospecific, and a type collection was designated (*Seler 2750*).

A few years later, Alice Eastwood (1909) published her comprehensive revision of *Castilleja* in Mexico and Central America, based largely on her studies at the Gray Herbarium (GH). Evidently, Eastwood saw none of the material from Seler's collections, and in her treatments of *Castilleja tapeinoclada* and *C. katakyptusa*, she simply quoted directly from Loesener's paper, without further comment or any citation of specimens seen by her. She accepted all of Loesener's names and made no further comments on their typifications. I have confirmed that no type material from Seler's collections is present at GH or at any of the other herbaria now housed at Harvard University (Walter Kittridge, pers. comm. 2005).

In their treatment of Scrophulariaceae in the Flora of Guatemala, Standley and Williams (1973), reduced var. *subglabra* and var. *hirta*, as well as the closely related *Castilleja katakyptusa*, to synonymy under *C. tapeinoclada*, but they made no further comment on its typification, simply repeating Loesener's typification of his two named varieties in the synonymy. Standley and Williams' interpretation of the Loesener's taxa stands today, and my herbarium studies of specimens from throughout the range of *C. tapeinoclada* confirm that the variants distinguished by Loesener are not geographically or ecologically consistent and likely represent random morphological variations commonly found in many *Castilleja* species.

Figure 1. *Castilleja tapeinoclada*, flowers and bracts. Photo by Fred Muller, Sierra de los Cuchumatanes, Depto. Huehuetenango, Guatemala, 15 May 2011.

Figure 2. *Castilleja tapeinoclada*, cluster of plants. Photo by Fred Muller, Sierra de los Cuchumatanes, Depto Huehuetenango, Guatemala, 25 May 2013.

In addition to the ambiguous nature of the typification of *Castilleja tapeinoclada* addressed above, it also appears that there are no extant specimens of any of the relevant Seler collections cited by Loesener, as Seler's primary collections were destroyed in the allied bombing of Berlin in World War II (C. Oberprieler at B, pers. comm., 2003; Harvard University Herbaria Botanist Database). Although some duplicates of Seler's collections are extant, my extensive efforts to locate any of the specimens designated by Loesener in all herbaria known to house at least some Seler collections (A, CAS, DS, F, GH, K, MEXU, MO, NY, US) have been completely unsuccessful. Internet searches of collection databases and type registries have proved equally fruitless. Finally, the three Seler type collections associated with *C. tapeinoclada* do not appear to be among the historical type images obtained by J.F. Macbride from European herbaria and now housed at F.

In order to provide an unambiguous type collection for *Castilleja tapeinoclada* for the *Castilleja* treatment in a forthcoming volume of the Flora Mesoamericana, the following neotypification is proposed, based on a gathering that is typical of individuals of this species, originates from the general region of the original type collections, contains ample plant material, and is distributed to several major herbaria.

CASTILLEJA TAPEINOCLADA Loes., Bull. Herb. Boiss., ser. 2, 3: 285. 1903. **NEOTYPE** (here designated): **Guatemala. Dept. Huehuetenango**: Sierra de los Cuchumatanes, at Chemal at km 318 on Ruta Nac. 9N, frequent in grassy meadow in black loam soil, ca. 3380 m, 4 Aug 1959, *J.H. Beaman 3073* (TEX!, isoneotypes: UC!, US!). Figure 3.

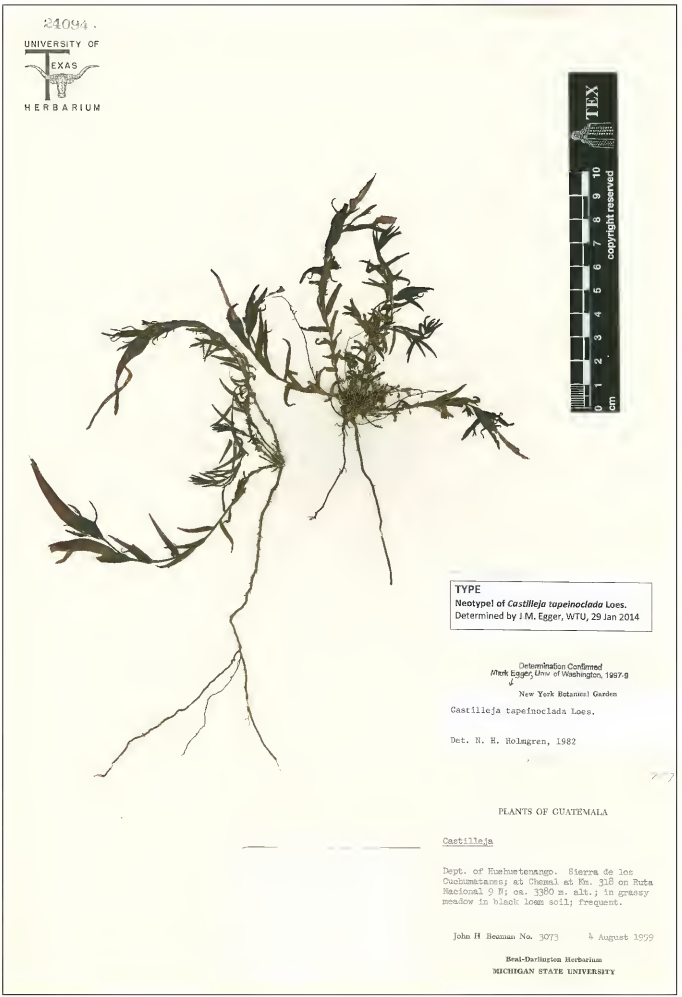

Figure 3. Neotype of *Castilleja tapeinoclada* Loes., *Beaman 3073* (TEX).

Castilleja tapeinoclada Loes. var. *subglabra* Loes., Bull. Herb. Boiss., ser. 2, 3: 285. 1903. **Type**: **Guatemala**. **Dept. Quezaltenango** [= Quetzaltenango]. In pratis alpinis supra Totonicapam [=Totonicapan] in 3000 m altitude, Sep [1896], *E.G. Seler 2357* (holotype: B, apparently destroyed).

Castilleja tapeinoclada Loes. var. *hirta* Loes., Bull. Herb. Boiss., ser. 2, 3: 285, 1903. **Type**: **Guatemala**. **Dept. Quezaltenango** [= Quetzaltenango]. In pratis alpinis ad Ziha in 2840 m altitude, Jun [1896], *E.G. Seler 2933* (holotype: B, apparently destroyed).

Castilleja katakyptusa Loes., Bull. Herb. Boiss., ser. 2, 3: 286. 1903. **Type**: **Guatemala**. **Dept. Huehuetenango**. In pratis et silvestribus in jugo montium inter Todos los Santos et Chiantla in 3000 m altitude, Sep [1896], *E.G. Seler 2750* (holotype: B, apparently destroyed).

Castilleja tapeinoclada is an uncommon to locally abundant endemic of high elevation meadows and often heavily grazed pastures in the highlands of western Guatemala from 2,700-4,000 meters elevation. In the Flora of Guatemala (op. cit.), Standley and Williams described it as "occasional," but recent observers (e.g. Fred Muller, pers. comm. 2014) indicate that it is quite common, forming large, conspicuously colorful displays in at least some portions of the Sierra de los Cuchumatanes (Figs. 1 and 2). It is unknown if this discrepancy indicates actual population increases in recent decades, but this species seems to do well on heavily grazed lands, perhaps benefiting from the reduction in competition from more palatable plants. This abundance on grazed pastures is noted on several herbarium collection labels and by local observers. *Castilleja tapeinoclada* has been collected in flower during all months from mid-May to early January in the Departments of Chimaltenango, Huehuetenango, San Marcos, Quetzaltenango, Solala, and Totonicapan.

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STATUS OF *AMELANCHIER ARBOREA* (ROSACEAE) IN TEXAS

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ABSTRACT

For over 75 years, *Amelanchier arborea* has been mentioned as a natural part of the flora of Texas, apparently without satisfactory documentation. The most recent listing of the vascular plants of Texas did not include the species as being in the state. Recent literature, herbarium, and field study have resulted in the discovery and collection of the species in Newton County, thus providing conclusive evidence of the occurrence of the species in the state.

Although much has been written about *Amelanchier arborea* (F. Michx.) Fernald (Rosaceae) in Texas, the species has never been convincingly documented as part of the state's flora. Following is a summary of the important publications detailing the unusual literary history of the status of the species in Texas. Note that publications citing *A. arborea* as being in Texas have several similarities:

* records seem borrowed from earlier works,
* the stated distributions, although very general, don't always agree,
* where only trees are included, the species may have been excluded for not meeting the stated definition of a tree, and
* none cites a specimen or references a publication citing a specimen

Cory and Parks (1937) apparently treated *Amelanchier arborea* under the name *A. canadensis* (L.) Medik., a misapplication of that name. The stated distribution of the species included ecological areas 1 and 4 of that work, where area 1 was the Timber Belt, known today as the Pineywoods, and area 4 was the Blackland Prairie, which comprised the vegetational regions currently known as the Post Oak Savannahs, Blackland Prairies, and Cross Timbers and Prairies (Gould 1962). Cory and Park's (1937) expanded definition of area 4 seems responsible for the Hatch et al. (1990) and Diggs et al. (1999) references citing *A. arborea* as occurring in today's area 4 (Blackland Prairies).

When Fernald (1941) proposed the new combination *Amelanchier arborea* (based on *Mespilus arborea* F. Michx., Hist. Arb. Amer. Sept. 3: 68, t. 11. 1810), Texas was not included as part of the distribution; he also later noted (Fernald 1950) that the westernmost known localities were in Oklahoma and Louisiana. Gould's (1962) Texas checklist did not list the species, while Correll and Johnston (1970), in the *Manual of the Vascular Plants of Texas*, noted that *Amelanchier arborea* occurs in "rich woodlands along streams, in thickets and on open wooded slopes in n.e. Tex." Johnston (1990), in a checklist updating Correll and Johnston (1970), left the entry on *Amelanchier arborea* unchanged.

The species was listed in Little (1953) as present in eastern Texas. Little defined trees as "woody plants having one erect perennial stem or trunk at least 3 inches in diameter at breast height ($4\frac{1}{2}$ feet), a more or less definitely formed crown of foliage, and a height of at least 12 feet." Little (1977) did not map the species in Texas in the *Atlas of U.S. Trees vol. 4, Minor Eastern Hardwoods*. No reason is given for the change from Little (1953), but it may be related to a lack of a specimen from Texas or failure to meet the definition of a tree.

In *A Field Guide to Texas Trees*, Simpson (1988) mentioned the following: "A*melanchier arborea* (Service-berry) at Monroe, Louisiana, is a 25-foot-tall tree. Yet the only one I have seen in the wild in Texas was scarcely 3 feet tall and flowering profusely. Seedlings grown from the Texas species for ten years remain only 3 feet tall." The essence of his statement is that *A. arborea* did occur in Texas but was not treated by him because it did not meet the definition of a tree — having a single or multiple trunk growing to 12 feet or more in height and being definitely woody. Neither a voucher specimen nor locations of the original plants grown by Simpson were mentioned.

The checklist of Hatch et al (1990) included the species as occurring in vegetational areas 1 and 4 — in this work, area 1 is the Pineywoods of east Texas, while area 4 is the Blackland Prairie, an unlikely site for *A. arborea*, indicating perhaps that the distribution was copied from Cory and Parks (1937) but without emendation of the differences between the two area 4s. In yet another Texas checklist, Jones et al. (1997) cited the species in Texas as var. *arborea*, but they did not provide distributional data. The species was included in flora of north-central Texas by Diggs et al. (1999) on the basis of the citation in Hatch et al. (1990). In Turner et al. (2003) *A. arborea* is neither mapped nor cited in the index. USDA, NRCS (2014), however, maps the species in Texas but does not include a county distribution map (as done with other Texas species). The Texas county-level maps in USDA, NRCS are apparently taken from Turner et al. (2003), which would explain a lack of a map for *A. arborea*. Finally, Kartesz (2013) does not map the species in Texas.

Kartesz (2013), however, has mapped *Amelanchier arborea* as present in two counties of southeast Oklahoma bordering Texas along the Red River and also in three parishes of Louisiana contiguous with Texas, presumably following Thomas and Allen (1998) in their Louisiana Atlas. This nearby distribution, in some instances very few miles distant from Texas, seemed indicative of the species' presence in Texas, thus our interest. Initially, but without results, the following herbaria were surveyed in an attempt to locate an existing specimen: SMU-BRIT, TEX-LL, TAMU, and TRACY.

Relocation of *Amelanchier arborea* in Texas

We successfully located several specimens of *Amelanchier arborea* and here cite two collections to document its presence in Texas. Although the plants were located and collected at the very end of the autumn (18 December) and the plants were dormant, we were able to observe and collect buds and leaves still attached — both used to confirm the identity of the species. Both of the plants from which vouchers were collected were about 2 meters tall, slender understory trees apparently similar in habit to those earlier observed by Simpson. Perhaps because of their near-leafless condition, we were able to locate only three individuals.

Voucher specimens: **Texas**. Newton County: 4.7 mi W of Mayflower Community at the jct. of Hwy R255 and Hwy 87 on Hwy R255, headwaters of Little Cow Creek at the jct. of R255, downstream 0.4 mi (site 1, 31° 3' 41.76" N, 93° 47' 45.60" W), E side of Little Cow Creek on a terrace near the edge of creek, 18 Dec 2013, *Holmes, Singhurst,* and *Loos 15979* (BAYLU); 0.6 mi downstream (south) from above location (site 2, 31° 3' 38.98" N, 93° 47' 38.40" W), 18 Dec 2013, *Holmes, Singhurst,* and *Loos 15980* (BAYLU). Figures 1, 2.

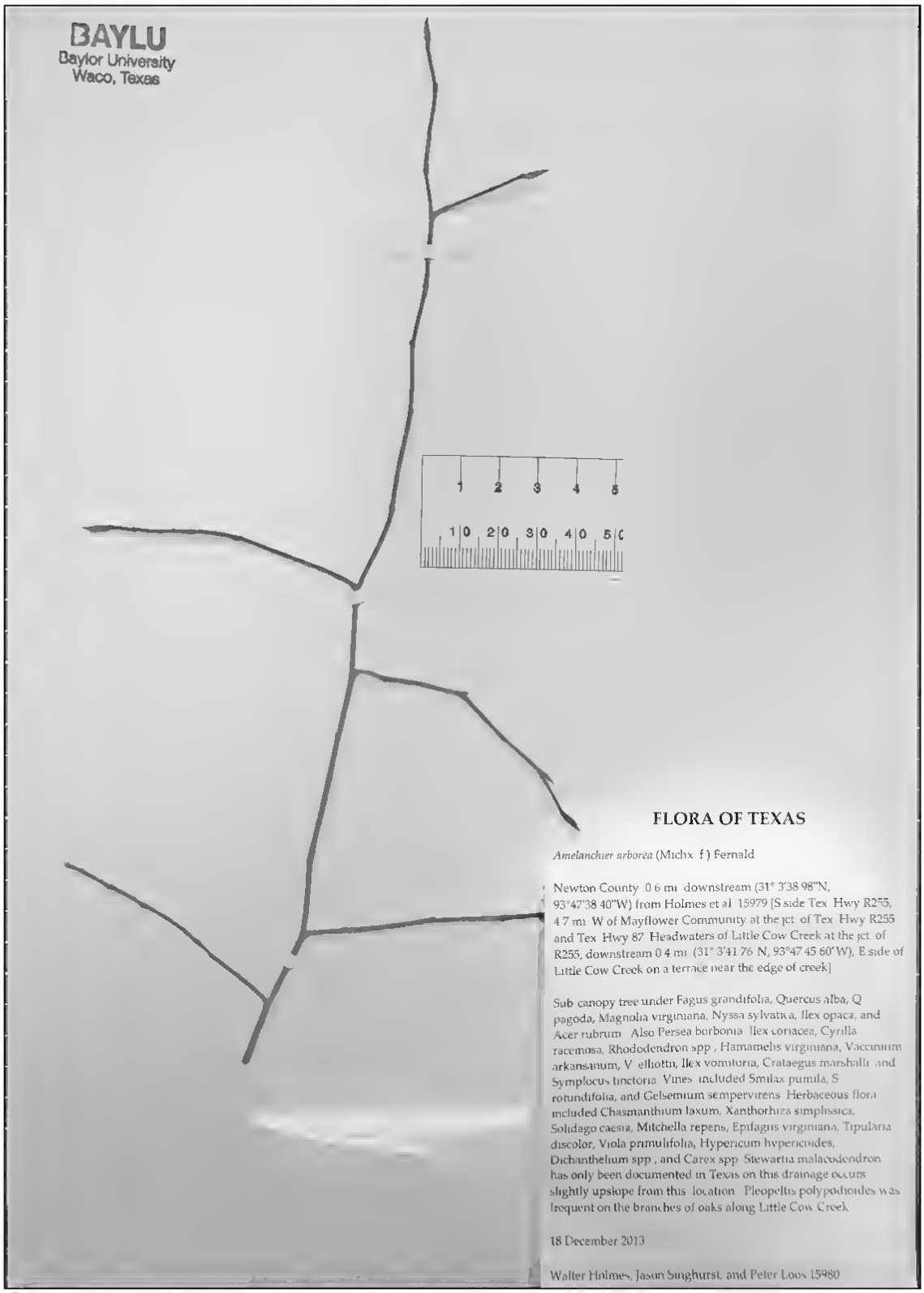

Figure 1 *Amelanchier arborea* (*Holmes, Singhurst,* and *Loos 15980*, BAYLU)

Figure 2. *Amelanchier arborea*. Leaf from dormant plant (*Holmes, Singhurst,* and *Loos 15980*, BAYLU).

Amelanchier arborea in Texas is a subcanopy tree growing under *Fagus grandifolia, Quercus alba, Q. pagoda, Magnolia virginiana, Nyssa sylvatica, Ilex opaca*, and *Acer rubrum*. Both sites also included *Persea borbonia, Ilex coriacea, Cyrilla racemosa, Rhododendron spp., Hamamelis virginiana, Vaccinium arkansanum, V. elliottii, Ilex vomitoria, Crataegus marshallii*, and *Symplocus tinctoria*. Woody vines in the vicinity included *Smilax pumila, S. rotundifolia*, and *Gelsemium sempervirens*. Herbaceous flora included *Chasmanthium laxum, Xanthorhiza simplicissima, Solidago caesia, Mitchella repens, Epifagus virginiana, Tipularia discolor, Viola primulifolia, Hypericum hypericoides, Dichanthelium* spp., and *Carex* spp. *Stewartia malacodendron*, a rare peripheral shrub species that has only been documented in Texas on Little Cow Creek, occurs slightly upslope from the *A. arborea* populations. *Pleopeltis polypodioides*, an epiphytic fern, was also frequent on the branches of oaks along the creek.

Amelanchier arborea is the second species of the genus documented for Texas. *Amelanchier utahensis* Koehne occurs in the Guadalupe Mountains of the trans-Pecos region (see Turner et al. 2003; Correll & Johnston 1970). A third species, *A. denticulata* (Kunth) K. Koch., as treated by Correll and Johnston (1970), is now referable to *Malacomeles denticulata* (Kunth) G.N. Jones (Turner et al. 2003).

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This research was facilitated by our botanical compadres of east Texas, both professional and amateur, who not only advised us of the presence of the species in Texas but also mentioned exactly where and, in this case, led us to the location. The authors are indebted to Guy Nesom for comments and suggestions. Darrell Vodopich of Baylor University processed the photographs.

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OVERLOOKED SECTIONAL NAMES OF NORTH AMERICAN ROSACEAE TRIB. POTENTILLEAE

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ABSTRACT

A series of overlooked infrageneric sectional names in Rosaceae trib. Potentilleae inadvertently but effective published by O.A. Stevens in 1959 are reported. Additional section names of potential nomenclatural significance were proposed by him in *Rosa*, *Rubus*, and *Spiraea* (Rosaceae) as well as *Grossularia*, *Heuchera*, and *Ribes* (Saxifragaceae), but these are not considered here.

Because of our decision to organize species of *Horkelia*, *Ivesia*, and *Horkelia* (Rosaceae Juss. trib. Potentilleae Sweet) within sections for a forthcoming volume of *Flora of North America*, we attempted to account for all of the infrageneric names applied to the members of the tribe in this region. Sections that had been established for North American *Potentilla* were mostly based on a subset of Per Axel Rydberg's unranked "groups," the majority of which had been validly published by Rydberg in the *Bulletin of the Torrey Botanical Club* (Rydberg 1896b, 1896c, 1896d, 1896e, 1897), in his 1898 doctoral dissertation, *A Monograph of North American Potentilleae*, or his 1908 treatment of the rose family in *North American Flora*. Many of these "groups" were in turn derived from various infrageneric units (some invalid) introduced by Johann Georg Christian Lehmann (1856) in his monumental classic *Revisionem Potentillarum*, which Rydberg (1896a: 244; 1898: 2) considered to be the basis for his own revision. Many of Rydberg's unranked names were assigned sectional rank by subsequent authors, notably Nelson (1909), Juzepczuk (1941), and Johnston (1985), sometimes unintentionally and often with redundancy.

As a result of our efforts, we located one previously overlooked place where some of Rydberg's names had been validated as sections (Ertter 2008; Nelson 1909) and made several such validations ourselves (Ertter & Reveal 2007). We failed to notice, however, that Orin Alva Stevens (1885–1979), in a 1959 index to volume 22 of *North American Flora*, had inadvertently validated, as sections, all the infrageneric names proposed by Rydberg in this work. In the majority of instances, Stevens's publication merely changes the authorship and bibliographic reference of sectional names we were already using. In a few cases, however, Stevens's earlier sectional names replaced later ones we had been using up to the galley stage of the *Flora of North America* manuscript.

Our purposes here are twofold. One is to report on the unlooked Stevens names in the trib. Potentilleae. The second is to alert workers that Stevens also validated a series of additional infrageneric names in Rosaceae (*Rosa*, *Rubus*, and *Spiraea*) and Saxifragaceae (*Grossularia*, *Heuchera*, and *Ribes*). We have made no attempt to ascertain the potential changes in names and/or authorships of sectional names in those genera.

Validation of the unranked Rydberg names was accomplished in a twofold process. First, Stevens assigned a rank to an otherwise effectively and validly published unranked name. Second, because this was an index to the unranked names used in 1908 that may or may not have been the first place that Rydberg validated the name, Stevens's error in the citation of the basionym is correctable under Art. 41.8(a) of the *Code* (McNeill et al. 2012) inasmuch as Rydberg, in 1908, effectively and validly published the names again.

In the following list, we report the newly discovered sectional names in *Horkelia* Cham. & Schltdl., *Ivesia* Torr. & A. Gray, and *Potentilla* L.

Horkelia Cham. & Schltdl. sect. *Californicae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Californicae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 121. 25 Nov 1898 via N. Amer. Fl. 22(4): 269, 271. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. californica* Cham. & Schltdl.

Horkelia Cham. & Schltdl. sect. *Capitatae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Capitatae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 122. 25 Nov 1898 via N. Amer. Fl. 22(4): 269, 272. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. capitata* Lindl.

Horkelia Cham. & Schltdl. sect. *Cuneatae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Cuneatae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 121. 25 Nov 1898 via N. Amer. Fl. 22(4): 269, 276. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. cuneata* Lindl.

Horkelia Cham. & Schltdl. sect. *Hirsutae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Hirsutae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 123. 25 Nov 1898 via N. Amer. Fl. 22(4): 269, 276. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. hirsuta* Lindl.

Horkelia Cham. & Schltdl. sect. *Sericatae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Sericatae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 123. 25 Nov 1898 via N. Amer. Fl. 22(4): 270, 278. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. sericata* S. Watson

Horkelia Cham. & Schltdl. sect. *Tenuilobae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Tenuilobae* Rydb. in N. Amer. Fl. 22(4): 269, 272. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. tenuiloba* Jordan

Horkelia Cham. & Schltdl. sect. *Tridentatae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 7. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Tridentatae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 122. 25 Nov 1898 via N. Amer. Fl. 22(4): 270, 279. 20 Nov 1908 [Art. 41.8(a)]. – T.: *H. tridentata* Torr.

Ivesia Torr. & A. Gray sect. *Eremicae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 8. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Eremicae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 124. 25 Nov 1898 via N. Amer. Fl. 22(4): 283, 284. 20 Nov 1908 [Art. 41.8(a)]. – T.: *I. eremica* (Coville) Rydb.

Ivesia Torr. & A. Gray sect. *Lycopodioides* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 8. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Lycopodioides* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 124. 25 Nov 1898 via N. Amer. Fl. 22(4): 283, 286. 20 Nov 1908 [Art. 41.8(a)]. – T.: *I. lycopodioides* A. Gray

Ivesia Torr. & A. Gray sect. *Setosae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 8. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Setosae* Rydb. in N. Amer. Fl. 22(4): 283, 290. 20 Nov 1908 [Art. 41.8(a)]. – T.: *I. setosa* (S. Watson) Rydb. [NOTE: This name has equal priority with *Potentilla* L. sect. *Saxosae* (Rydb.) O. Stevens, typified by *P. saxosa* Lemmon ex Greene, and while this has been transferred, as *Ivesia* sect. *Saxosae* (Rydb.) Ertter & Reveal, to that genus, the sect. *Setosae* has priority at the rank of section.]

Ivesia Torr. & A. Gray sect. *Unguiculatae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 8. 23 Sep 1959, based on *Horkelia* [infragen. unranked] *Unguiculatae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 120, 124. 25 Nov 1898 via N. Amer. Fl. 22(4): 283, 284. 20 Nov 1908 [Art. 41.8(a)]. – T.: *I. unquiculata* A. Gray

Potentilla L. sect. *Arenicolae* (Rydb.) O. Stevens in *N. Amer. Fl.* 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Arenicolae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 31. 25 Nov 1898 via N. Amer. Fl. 22(4): 293, 294, 308. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. newberryi* A. Gray

Potentilla L. sect. *Biflorae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Biflorae* Rydb. in Bull. Torrey Bot. Club 24: 13. 28 Jan 1897 via N. Amer. Fl. 22(4): 294, 335. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. biflora* Willd. ex D.K.F. Schltdl.

Potentilla L. sect. *Brevifoliae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Brevifolia* Rydb. in Bull. Torrey Bot. Club 23: 306. 20 Aug 1896, via N. Amer. Fl. 22(4): 294, 336. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. brevifolia* Nutt. ex Torr. & A. Gray

Potentilla L. sect. *Candicantes* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Candicantes* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 32. 25 Nov 1898 via N. Amer. Fl. 22(4): 294, 339. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. candicans* Humb. & Bonpl. ex D.K.F. Schltdl.

Potentilla L. sect. *Candidae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Candidae* Rydb. in N. Amer. Fl. 22(4): 294, 315. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. candida* Rydb.

Potentilla L. sect. *Concinnae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Concinnae* Rydb. in Bull. Torrey Bot. Club 23: 431. 25 Nov 1896 via N. Amer. Fl. 22(4): 294, 328. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. concinna* Richardson

Potentilla L. sect. *Frigida* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Frigida* Rydb. in Bull. Torrey Bot. Club 23: 301, 304. 20 Aug 1896, via N. Amer. Fl. 22(4): 294, 333. 20 Nov 1908 [Art. 41.8(a)]. – LT.: *P. flabellifolia* Hook., to be designated.

Potentilla L. sect. *Heptaphyllae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, as "Heptophyllae", based on *Potentilla* [infragen. unranked] *Heptaphyllae* Rydb. in N. Amer. Fl. 22(4): 294, 310. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. leptophylla* Rydb.

Potentilla L. sect. *Heterosepalae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Heterosepalae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 21, 23. 25 Nov 1898 via N. Amer. Fl. 22(4): 293, 303. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. heterosepala* Fritsch

Potentilla L. sect. *Horridae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Horridae* Rydb. in N. Amer. Fl. 22(4): 294, 322. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. heterosepala* Fritsch

Potentilla L. sect. *Longipedunculatae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Longipedunculatae* Rydb. in N. Amer. Fl. 22(4): 293, 320. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. longipedunculata* Rydb.

Potentilla L. sect. *Nuttallianae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Nuttallianae* Rydb. in N. Amer. Fl. 22(4): 293, 294, 310. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. nuttallii* Lehm.

Potentilla L. sect. *Obovatifoliae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Obovatifoliae* Rydb. in N. Amer. Fl. 22(4): 294, 321. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. obovatifolia* Rydb.

Potentilla L. sect. *Pectinisectae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, as "Pectenisectae", based on *Potentilla* [infragen. unranked] *Pectinisectae* Rydb. in N. Amer. Fl. 22(4): 294, 316. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. nuttallii* Lehm.

Potentilla L. sect. *Permolles* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Permolles* Rydb. in N. Amer. Fl. 22(4): 294, 315. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. permollis* Rydb.

Potentilla L. sect. *Rubrae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Rubrae* Rydb. in N. Amer. Fl. 22(4): 293, 323. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. rubra* Willd. ex D.K.F. Schltdl.

Potentilla L. sect. *Saxosae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Horkelia* Cham. & Schltd. [infragen. unranked] *Saxosae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 121, 125. 25 Nov 1898 via *Potentilla* L. [infragen. unranked] *Saxosae* Rydb., N. Amer. Fl. 22(4): 294, 335. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. saxosa* Lemmon ex Greene

Potentilla L. sect. *Subcoriaceae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 23 Sep 1959, based on *Potentilla* [infragen. unranked] *Subcoriaceae* Rydb. in N. Amer. Fl. 22(4): 294, 320. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. subcoriacea* Rydb.

Potentilla L. sect. *Subviscosae* (Rydb.) O. Stevens in N. Amer. Fl. 22(7): 11. 3 Sep 1959, based on *Potentilla* [infragen. unranked] *Subviscosae* Rydb. in Mem. Dept. Bot. Columbia Coll. 2: 24. 25 Nov 1898 via N. Amer. Fl. 22(4): 294, 327. 20 Nov 1908 [Art. 41.8(a)]. – T.: *P. subviscosa* Greene

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LOMATIUM TARANTULOIDES (APIACEAE), A NEW NARROWLY ENDEMIC SPECIES FROM NORTHEAST OREGON

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ABSTRACT

Lomatium tarantuloides Darrach & Hinchliff, **sp. nov.**, is a narrow endemic of conservation concern growing primarily in shallow, gravelly, serpentine-derived soils in a small area of the Malheur, Umatilla, and Wallowa-Whitman National Forests in Grant County of northeastern Oregon. The species is distinguished from other members of the genus by leaf morphology, prostrate inflorescences and infructescences, fruit shape, and pedicel length. The presently recognized populations are primarily confined to small patches within a several km^2 area in the higher elevations of the Greenhorn Mountains in the Blue Mountain physiographic province. Populations are of densely clustered plants in sites often characterized by persistent rodent-perpetuated disturbance where the new species tends to display the highest biomass of any single vascular plant species present.

Lomatium is by far the largest genus in Apiaceae in North America. Several new species from the USA have been described over the last few years, including *L. ochocense* Helliwell (2010), *L. bentonitum* Carlson & Mansfield (Carlson et al. 2011), *L. pastoralis* D.H.Wagner ex Darrach & Wagner (2012), and *L. brunsfeldianum* McNeill (2012).

Collections of an unrecognized white-flowered *Lomatum* species were made by botanists Stuart Markow and Mark Darrach in the Greenhorn Mountains of northeastern Oregon in July 2002. The population at that site (type locality) is confined to shallow serpentine-derived gravelly lithosol soils at 2291 meters on a nearly flat aspect on the Umatilla National Forest. Subsequent morphological examination and comparison of specimens with reference material by Stuart Markow at the Rocky Mountain Herbarium (RM) and Mark Darrach at the Burke Museum Herbarium (WTU), Washington State University (WS), and Oregon State University (OSC, ORE, WILLU) suggested these collections represented a hitherto undescribed species with morphological similarities to the recently described *L. pastoralis*.

Recent molecular genetic work conducted in 2011 and 2012 as part of a broader investigation into the genetics of *Lomatum* by Emma George (College of Idaho), Jim Smith (Boise State University), and Donald Mansfield (College of Idaho) has confirmed the 2002 collections to be a genetically distinct entity, but in a separate clade relative to *L. pastoralis* (George et al., in press).

Since its initial discovery, new populations of the species have been found on similar serpentine substrates; all but two are within a few kilometers of the type locality. Two additional yellow-flowered populations on an acidic volcanic mudflow substrate are also now known from approximately 23 kilometers north-northeast of the type locality. Aside from the yellow flower color, plants from these two populations do not differ significantly from those at the type locality.

Measurements in the description below represent a combination of characters derived from both herbarium material and live plants.

Lomatium tarantuloides M.E. Darrach and C.E. Hinchliff, **sp. nov.** Figures 1, 2, 3. **TYPE**: **USA. Oregon**. Grant Co.: open lithosol area on serpentine adjacent to DuPratt Spring, ca. 3.5 km E of summit of Boulder Butte, T10S R34E NW ¼ of NE ¼ Sec.10, 44º 44' 0.773" N; 118º 36' 15.152" W, abundant in vernally moist open gravelly serpentine lithosol on flat or gentle southerly aspects, elev. 2291 m (7215 ft), 22 Jul 2010, *M.E. Darrach 794* (holotype: WTU; isotypes: OSC, WS, RENO, NY, UMA, US).

Lomatium tarantuloides combines character states distinct from its immediately associated and regionally contiguous congeners and all other recognized members of the genus. The following characters are particularly diagnostic: prostrate inflorescences and infructescences, usually white flowers, involucel bracts usually completely lacking or very poorly developed, fruits elliptical with narrow wings, and small (usually 5 mm in length), and pedicels short (usually about 2.5 mm in length).

Herbs: perennial, long-lived, non to faintly aromatic, glabrous, acaulescent (caulescent), 0.5–17.0 cm in height with typical plants approximately 5cm in height when in mature fruit. **Root**: a simple to rarely bifurcate taproot, terete, 3.4–12.4 cm long, 1.6–10.0 mm wide, surmounted by a simple subterranean root crown and a narrow prominent terete subterranean pseudoscape, 15.0–75mm long that is typically single, but can be as numerous as 7 in the oldest specimens. The point of attachment between root crown and pseudoscape typically is somewhat swollen. Root crown annual scars, when clearly discernable, 5–55 in number reflecting approximate plant age. **Leaves**: old sheathing leaf bases entirely absent, leaves 2–29, most typically 3, venation obscure, glabrous, compound, ternate to biternate-pinnate to irregularly pinnate or irregularly partially bipinnate, 1.5–9.1 cm wide, 1.1–9.5 cm in length. Petioles 0.4–5.0 cm long with variably developed winged basal portions, winged bases herbaceous with variably green to blackish-purple anthocyanic coloration at the base and bearing entire to occasionally weakly serrate scarious margins that become stramineous and chartaceous with age, prominent nerves on leaves with winged petioles 4–13. Reduced, usually once pinnate axillary leaves often present, petioles of these leaves enclosed within broad-winged bases of larger primary leaves, wings lacking or minimally developed, usually entirely lacking nerves. Pressed leaves usually about equally as broad as wide, the leaf outline quadrate, rhombic, axillary leaves narrowly rhombic. Leaflets spreading, not overlapping, entire, narrowly elliptical to very narrowly oblanceolate to spatulate to, occasionally, linear-filiform, ultimate segments 2–43 mm long, 0.4–3.8 mm wide. **Inflorescences**: compound, involucre none, numbering up to 19 in old, long-established plants, but typically 2 or 3, shorter axillary peduncles occasionally present. Peduncles prostrate to weakly ascending, terete and typically weakly ribbed, usually deep blackish-purple at the base, R:77 G:5 B:34 (Colorpicker 2014). Peduncle length 20–110 mm in flower with typical specimens 60–70 mm, greatly exceeding the leaves as the inflorescence matures with typical increases in peduncle length of approximately 70% at maturity relative to when plants are at anthesis. Rays 2–23, dimidiate and unequal in length in flower, grossly so in fruit. Minimum ray length per inflorescence 1.5–5.5 mm, maximum per inflorescence 8.5–29.5. Shortest rays usually bearing umbellets with entirely male flowers. These short, staminate umbellets are frequently somewhat contorted and are clustered at the umbel center, they are irregularly deciduous by maturity and tend to

bear fewer flowers. The longer rays bear umbellets that are a mixture of male, female and, occasionally, perfect flowers. Male flower pedicels smooth, glabrous, 1.3–2.1 mm in length with typical values about 1.7 mm, female and perfect flower pedicels smooth, glabrous, 0.6–2.3 mm with typical values about 1.2 mm. **Involucel**: bracts green, herbaceous, narrow to linear, bract number 0–8 and, when present as 3 or more, irregularly dimidiate. Of 205 umbellets evaluated for this character approximately 60% had no involucel bracts at all and an additional 31% had only one or two. Involucel bracts 0.6–3.2 mm in length, 0.1–0.3 mm in width, glabrous, free to base, often with a well-developed mid-vein. **Flowers**: primarily polygamomonoecious on most plants, but some plants are andromonoecious, glabrous 7–34 per umbellet with values of 15–20 typically encountered, petals bright white to greenish-white with green mid-nerve and notably bright yellow petals in one population, 0.8–1.3 mm long, 0.6–1.0 mm wide, ovate with an adaxially strongly incurved short apiculus; anthers rose-purple to purple on plants with white flowers, pale yellow on plants with yellow flowers, stylopodia nectaries purple or green on plants with white flowers and green on plants with yellow flowers. Styles 0.8–1.1 mm, strongly curved, outwardly divergent; ovaries green and glabrous. **Fruit**: hemispherically arranged with 0–16 fruit per umbellet; 7 or 8 being the most commonly encountered numbers, the longer rays usually considerably more fecund, pedicels spreading-ascending to semi-erect, 0.4–7.4 mm with typical values of about 2.5 mm encountered on most specimens. Fruits glabrous, 3.7–6.9 mm long with typical material about 5.0–5.5 mm in length, 1.5–2.7 mm wide with typical values approximately 2.0 mm. Fruit wing width 0.2–0.35 mm, not obviously thickened, strongly dorsiventrally compressed with rounded base and distal obtuse margin. Fruit shape elliptical, elliptical-ovate to oblong, color greenish tan in the intervals. Dorsal fruit surfaces with 2–4 (usually 3) well-develop nerves flush with the fruit surface; vittae obscure, 1–3 in the intervals, 0–3 along the commisure, 1–3 on the wings. Carpophore cleft to the base, persistent. A composite illustration is provided in Figure 1 and specimen photographs are in Figures 2 and 3.

Etymology. The epithet "tarantuloides" alludes to the dense, web-like interweaving of the prostrate, early-senescent infructescence peduncles of the closely spaced plants. The name "spider biscuitroot" is suggested as a common name.

Habitat. *Lomatium tarantuloides* is known only from flat to gently sloping southerly to easterly aspects. The plants occupy ephemerally, moist to wet, shallow soils primarily on serpentine/peridotite-derived gravelly sites that become dry and largely barren by mid-late summer. The two known yellow-flowered populations occupy sites with similar characteristics and soils with analogous textures, but with substrates of acidic volcanic mudflow parentage. The known sites all show strong evidence of a persistent, fossorial rodent-induced soil bioturbation regime.

Range. The species is known from a total of 8 very restricted localities. Six of these are at higher elevations in the Greenhorn Mountains, ranging elevation from approximately 1616 meters to 2317 meters. The type locality and one other site are on the Umatilla National Forest, four sites are on contiguous adjacent lands of the Malheur National Forest, and two sites are on lands of the Wallowa-Whitman National Forest. Populations most distant from the Greenhorn Mountains are just east of Moon Meadows in Grant County on the Umatilla National Forest at approximately 1800 meters elevation. One other apparently small population in the Trout Meadows area (adjacent to the Moon Meadows population) is on the Wallowa-Whitman National Forest and needs to be relocated and properly characterized.

Paratypes. **Oregon**. Grant Co.: Princess Trail, ca 150 yards SW of Dupratt Spring, ca 7.5 air mi SW of Granite, OR, T10S R34E NE ¼ of NW ¼ Sec. 3, 2256 m (7,400 ft), 9 Jul 2002, *Markow 12358* (OSC, RM); Trout Meadows, 20 feet S of FS road 52, ca 100 yards SE of Umatilla National Forest boundary, ca 10 air mi NW of Granite, OR 1616 m (5300 ft), 8 Jun 2003, *Markow 12473* (OSC, RM); Trout Meadows, 20 feet S of FS road 52, ca 100 yards SE of Umatilla National Forest

boundary, ca 10 air mi NW of Granite, OR, T7S R35E Sec. 13 SW, 1616 m (5300 ft), 26 Jun 2003, *J. Wood 7778* (OSC), along both sides of Blackeye Trail, ca 0.5 air mi E of intersection with FS Road 2010, Malheur National Forest, T10S R34E N ½ Sec. 24, 1951 m (6400 ft), 26 Jun 2003, *Markow 12491* (OSC, RM), 2 air mi S of Vinegar Hill near trailhead of Blackeye Trail on scabs and open areas both E and W of FS road 2010, T10S R34E SW ¼ of NE ¼ Sec. 24, 1977 m (6483 ft), 1 Jul 2003, *Markow 12494* (OSC, RM), 0.8 km S of Morning Mine site Greenhorn Mountains, 1919 m (6296 ft), 18 Jul 2011, *Darrach 683* (UMA), 1.3 km ESE of Moon Meadow along Packsaddle Trail, 1862 m (6110 ft), 25 Jul 2011, *Darrach 802* (UMA).

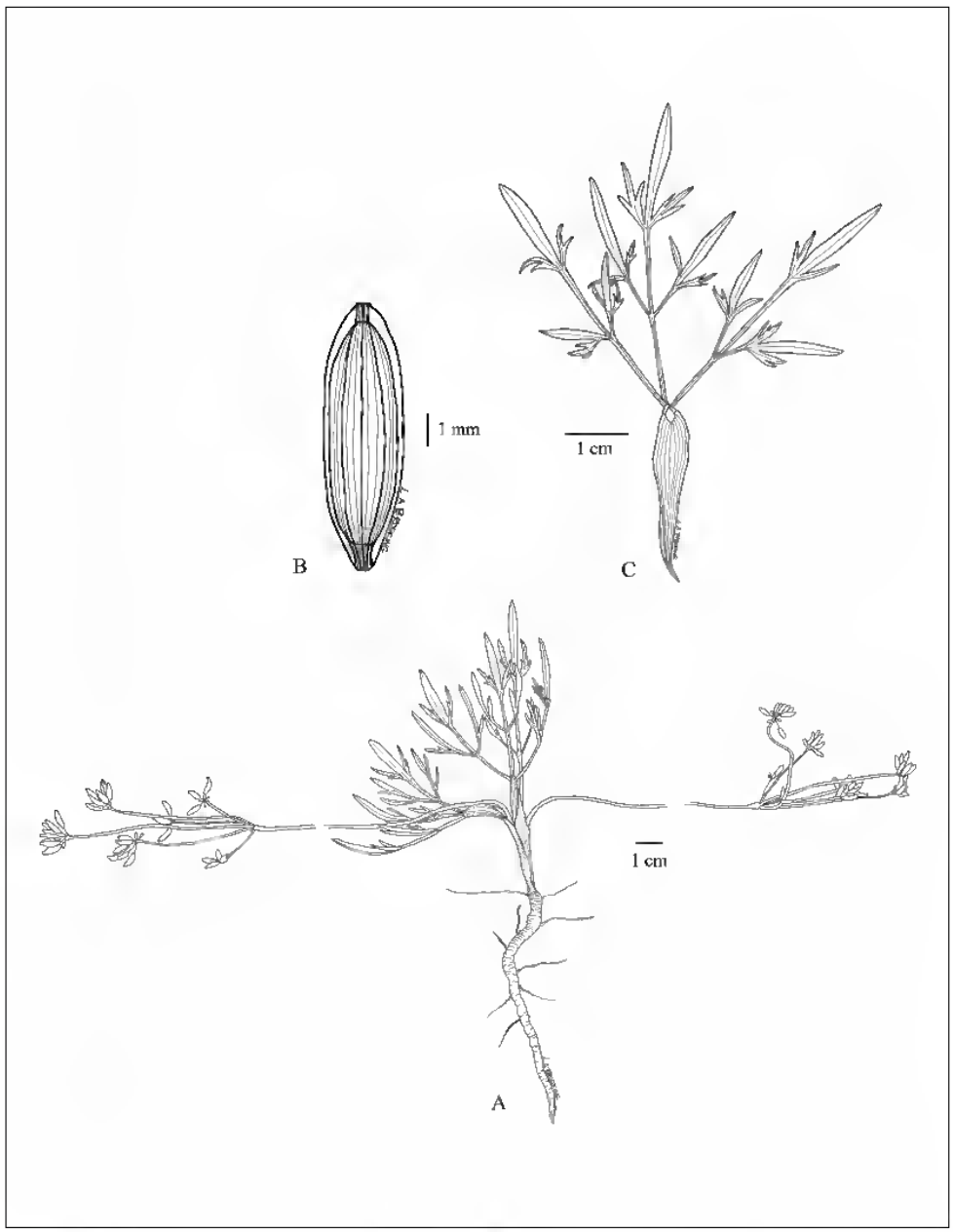

Figure 1. *Lomatium tarantuloides*. A. Habit of plant with grayed-out segment of infructescence peduncles representing missing segment necessary for illustrative purposes. B. Mature fruit. C. Typical leaf morphology.

Figure 2. *Lomatium tarantuloides*. Mature plant at anthesis in situ at type locality.

Figure 3. *Lomatium tarantuloides*. Mature plant at anthesis with typical taproot morphology.

Similarities and relationships

The species with which *Lomatium tarantuloides* is most likely to be confused are *L. leptocarpum* (Torr. & A. Gray) J.M. Coult. & Rose, the recently-described *L. pastoralis*, and *L. ultramaficum* D.W. Taylor & C. James (in press). *Lomatium leptocarpum* has bright yellow flowers, narrow nearly sessile fruits with a much higher aspect ratio, a well-developed involucel, more numerous leaflets, and ascending to upright inflorescences. The morphological similarities between *L. tarantuloides* and *L. pastoralis* are sufficient that it was initial thought that the two entities might be best treated as conspecific at infraspecific rank. Closer examination and recent molecular genetic evidence (George et al., in press) provide evidence that each should be recognized at the specific rank. *Lomatium pastoralis* always has bright yellow flowers, longer (on average) fruits, wider ultimate leaflets, and inflorescence peduncles that are strongly decumbent proximally, becoming ascendent to fully erect distally. *Lomatium ultramaficum*, recently discovered from Shasta County, California, also is confined to an ultramafic substrate. These plants are quite similar to *L. tarantuloides* but possess, on average, considerably longer and wider fruits, a light yellow flower color, and persistent leaf bases from previous growing seasons. The distance of many hundreds of air kilometers between the populations in a genus that is generally recognized as strongly limited in the scale of its areal seed distribution potential (Marisco & Hellman 2009) also provides a strong argument for *L. tarantuloides* and *L. ultramaficum* being of two distinct species.

Lomatium tarantuloides (under the designated placeholder "*Lomatium* sp. nov. F") is included in a molecular phylogenetic analysis addressing species-level relationships in *Lomatium* and related genera (George et al., in press). In that study, *L. tarantuloides* is placed with strong support in a small clade including another narrow endemic species known only from a small population in the Cascade Mountains of Washington state (*Lomatium* sp. nov., in prep.). Interestingly, *L. tarantuloides* is not indicated to share a close phylogenetic affinity with the recently described *L. pastoralis*, despite significant morphological similarity between them. As recognized by George et al. (in press) as well as preceding studies (Downie et al. 2002, 2010; Sun & Downie 2010a, 2010b), the phyletic placement of *L. tarantuloides* reflects an increasingly supported pattern in which apparent morphology-based taxonomic alliances within the clade including *Lomatium* and related genera do not translate accordingly when applying molecular phylogenetic analytical scrutiny.

Recognition that traditional morphological approaches to species circumscriptions may be of reduced reliability as an estimator of evolutionary relatedness in *Lomatium* and allied Apiaceae genera has significant taxonomic implications. Stronger consideration of the utility of genetic sequence data, ecological setting (e.g. substrate preferences), and biogeographic considerations may be critical for species delimitation and the recognition of lineages that merit conservation efforts. This has particular relevance for taxonomists as well as biodiversity managers in western North America, where Apiaceae constitutes a significant element of local floras. Indeed, the integration of non-morphological data has been an important avenue through which several distinct entities in this group have been recognized (George et al. in press; Carlson et al. 2011; Lesica & Kittelson 2013), and these approaches hold promise for the resolution of difficult groups such as *Lomatium triternatum* complex (George et al. in press; Lesica & Kittelson 2013).

Phenology, ecology, and conservation

Lomatium tarantuloides emerges each year primarily as a function of the timing of melt-back of the mountain snow pack. In low precipitation years this may occur as early as late May or the beginning of June, occasionally as late as mid-July. Flowers are at or near anthesis by mid-July in most years. The plants rapidly senesce thereafter, seed is fully dispersed by mid-August, and the plants become largely unrecognizable on the landscape by mid to late August.

The species typically occurs in dense populations on non-forested substrates, where it is usually the dominant vascular plant species. Associated vascular plant taxa documented to co-occur

with *Lomatium tarantuloides* include these: *Abies lasiocarpa, Achillea millefolium, Achnatherum lemmonii* subsp. *lemmonii, Achnatherum nelsonii* subsp. *dorei, Aconogonon phytolaccifolium, Allium campanulatum, Dicentra uniflora, Fritillaria pudica, Gayophytum humile, Lewisia pygmaea, Ligusticum grayi, Nothocalais alpestris, Perideridia bolanderi, Polygonum majus, Polygonum minimum, Ranunculus alismifolius* subsp. *davisii*, and *Sanicula graveolens*.

Observations of *Lomatium tarantuloides* populations indicate that it is an early seral occupant of bioturbated, non-forested landscapes. As soil push mounds and under-snowpack winter season rodent trace soil casts indicate, the primary source of persistent disturbance at the type locality and other population sites appears to be provided by active robust populations of the fossorial northern pocket gopher *Thomomys talpoides*. As long as these rodent populations persist at the population sites, the bioturbation activities of these small mammals create an ideal, albeit temporally unstable, disturbance regime that supports promotion of reproductive *L. tarantuloides* populations. However, as climate change effects reduce both the amount and duration of mountain snow packs in the region (Barnett et al. 2005), the continuing ability of these burrowing rodents to provide a persistent source of disturbance comes into question.

While summer domestic sheep usage is now entirely absent from most of the region, the area from which *Lomatium tarantuloides* populations are known was subjected to intensive sheep grazing from approximately 1890 through to the early 1930's (Langford 1996). This history echoes strongly in the character of the vegetation in the area (Darrach pers. observ.; Johnson pers. comm.), with nearly all of the shallow soil non-forested areas strongly departed ecologically from what are considered to be pre-settlement vegetation patterns. This grazing history also apparently produced a persistent source of disturbance that likely benefitted the fecundity of the *L. tarantuloides* populations. *Lomatium* species are, as a generality, unpalatable to livestock, and this may well have been an additional factor in keeping the species viable under strong herbivore pressure (Darrach pers. obs.; Utah State University 2013). As snowpack and, presumably, associated rodent activity, decline, a management strategy employing targeted domestic sheep or goat grazing in the populations may be of value in keeping populations of *L. tarantuloides* viable.

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LYSIMACHIA LATIFOLIA (MYRSINACEAE), AN OVERLOOKED NOMENCLATURAL CHANGE

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ABSTRACT

Lysimachia latifolia (Hook.) Cholewa is a new combination for the overlooked *Trientalis latifolia* Hook.

Phylogenetic relationships within Primulaceae s.l. examined by Anderberg and Stähl (1995) led to extensive reevaluation of the entire Lysimachieae clade. Some years later, Anderberg and colleagues (Anderberg et al. 2007; Källersjö et al. 2000; Manns & Anderberg 2005, 2007a, 2007b; Martins et al. 2003; and others) clearly showed that the traditionally segregated genera of *Anagallis*, *Glaux*, *Trientalis*, and others were specialized taxa derived from within *Lysimachia*. As a result generic realignments were necessitated.

Glaux maritima was merged in *Lysimachia* by Banfi et al. (2005) to become *Lysimachia maritima* (L.) Gelasso, Banfi, & Soldano. Manns and Anderberg (2009) subsequently published the necessary new combinations, along with typification comments for *Anagallis*, *Pelletiera*, and *Trientalis*. Within the North American flora, the following changes were made:

Anagallis arvensis L. became *Lysimachia arvensis* (L.) U. Manns & Anderb.;
Anagallis foemina Mill. became *L. foemina* (Mill.) U. Manns & Anderb.;
Anagallis monelli L. became *L. monelli* (L.) U. Manns & Anderb.;
Anagallis pumila Sw. became *L. ovalis* (Ruiz & Pav.) U. Manns & Anderb.;
Centunculus (*Anagallis*) *minimus* L. became *L. minima* (L.) U. Manns & Anderb.;
Trientalis borealis Raf. became *L. borealis* (Raf.) U. Manns & Anderb.; and
Trientalis europaea L. became *L. europaea* (L.) U. Manns & Anderb.

The nomenclatural updates were incomplete, however, omitting *Trientalis latifolia* Hook. This was understandable since this taxon has sometimes been included within *T. borealis* or *T. europaea*. In the Flora of North America treatment, Cholewa (2009) kept *T. latifolia* as a distinct species, thus the following new combination is proposed.

LYSIMACHIA LATIFOLIA (Hook.) Cholewa, **comb. nov.** *Trientalis latifolia* Hook., Fl. Bor.-Amer. 2(9): 121. 1838. *Trientalis borealis* Raf. subsp. *latifolia* (Hook.) Hultén, Ark. Bot., n.s., 7(1): 105. 1967. *Trientalis europaea* L. var. *latifolia* (Hook.) Torrey, Pacif. Railr. Rep. 4(5): 118. 1857. *Trientalis europaea* L. subsp. *latifolia* (Hook.) A.E. Murray, Kalmia 12: 25. 1982. **TYPE: USA. Washington**. [Clark Co.]: About Fort Vancouver, Walla-wallah [sic] River, *Tolmie s.n.* (holotype: K unconfirmed; isotype: GH digital image!).

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Grande A., J.R. 2014. Additional notes: Segregates from *Panicum* incertae sedis. Phytoneuron 2014-29: 1. Published 18 February 2014. ISSN 2153 733X

ADDITIONAL NOTES: SEGREGATES FROM *PANICUM* INCERTAE SEDIS

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The following notes provide additional explanation for the taxonomical novelties proposed in the recent paper on segregates from *Panicum* L. incertae sedis (Grande, Phytoneuron 2014-22: 1-6. 2014). Also included within a corrigendum are some minor errata in the text and literature.

a) Only validly published names were considered.

b) The genus *Coleataenia* Griseb. was considered in its narrowest sense, including only *C. prionitis* (Nees) Soreng (the type species) and the closely allied *C. petersonii* (Hitchc. & Ekman) Soreng and *C. beyeri* (Hitchc. & Ekman) J.R. Grande. *Sorengia* Zuloaga & Morrone is a superfluous name that explicitly includes the type of *Coleataenia*, while its type species (*Panicum agrostoides* Hitchc. & Chase) is both an illegitimate homonym and a superfluous name.

c) With the effective publication of this work, the remaining species in *Panicum* incertae sedis sect. *Laxa* (sensu Aliscioni et al. 2003) and *Panicum* subgen. *Agrostoidia* (Hitchc.) Zuloaga (sensu Zuloaga 1988[1987]) were validly removed from true *Panicum*.

d) Affinities within the Otachyriinae are, at the present time, fairly obscure and it is advisable to further study its generic limits. The criteria employed to delimit *Hymencahne* P. Beauv. vs. *Dallwatsonia* B.K. Simon were the presence of a thinly membranous upper anthecium, in which the palea is not concealed apically within the upper lemma, and stellate pithy tissue within the culms (both in *Hymenachne*). As the first character could be considered poorly understood (cf. Aliscioni et al. 2003) and the second remains to be fully surveyed throughout the subtribe (since the amount of pith may vary greatly between species), the proposed circumpscription of *Dallwatsonia* is to be considered only as provisional. Upper anthecium pubescence and ornamentation (not texture) could serve, once fully studied, as the most reliable characters to properly delimit the genera within that subtribe. Based on that character, *Dallwatsonia condensata* (Bertol.) J.R. Grande, *D. leptachne* (Döll) J.R. Grande, *D. longa* (Hitchc. & Chase) J.R. Grande, and *D. stagnatilis* (Hitchc. & Chase) J.R. Grande are related to *Hymenachne donacifolia* (Raddi) Chase and the species of the "*Grumosum* group" of Zuloaga et al. (1992), which also has flattened prickle hairs in the upper anthecium. *Dallwatsonia felliana* B.K. Simon, the type of the genus, has spikelets slightly longer than the remaining species (3.5–4 mm vs 1.2–3.2 mm).

e) The word advice, as used in the Acknowledgements, is not to be interpreted as a kind of supervision, participation, or approval of the new combinations made in the article, which was not sent to Fernando Zuloaga (SI) before its effective publication.

Corrigendum:

i) The abstract should include in line 4, before "*Coleataenia*" — "one new combination in"

ii) Morrone et al. 2012 was erroneously cited in the text as "2011" — thus Zuloaga et al. 2011 is not to be considered as a subsequent work and may be omitted from the cited literature.

iii) The gender of the epithet of the new combination proposed under *Acomisia* J.R. Grande is to be corrected, under Art. 32.2 and 23.5 of the Code, from neuter ("*grande*") to feminine ("*grandis*"). The correct name for the species is, thus, as follows: *Acomisia grandis* (Hitchc. & Chase) J.R. Grande.

Rodríguez, D. and T.F. Daniel. 2014. *Hygrophila costata* (Acanthaceae), nuevo registro para la flora de El Salvador. Phytoneuron 2014-30: 1–3. Published 4 March 2014. ISSN 2153 733X

HYGROPHILA COSTATA (ACANTHACEAE), NUEVO REGISTRO PARA LA FLORA DE EL SALVADOR

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RESUMEN

Se registra la ocurrencia de *Hygrophila costata* Nees & T. Nees en El Salvador por primera vez. Una descripción breve de la especie se acompaña fotografías de la planta y un mapa que muestra su distribución en el país. Actualmente 45 especies de Acanthaceae se conocen desde El Salvador.

ABSTRACT

Hygrophila costata Nees & T. Nees is reported from El Salvador for the first time. A brief description of the species is accompanied by photographs of the plant and a map showing its distribution in the country. Forty-five species of Acanthaceae are currently known from El Salvador.

La flora de Acanthaceae de El Salvador fue resumida por Daniel (2001, 2012), quien indicó la presencia de 44 especies nativas en el país. Daniel (2001) predijo que varias especies adicionales se pueden encontrar allí. En la exploración de campo realizada por el personal del herbario LAGU en la zona oriental de El Salvador, en el año 2013, se encontró una de estas especies, *Hygrophila costata* Nees & T. Nees, como primer registro para la flora del país. Para la identificación de la especie se realizó una revisión de literatura y material botánico de la familia Acanthaceae en los herbarios locales (LAGU y MHES); lastimosamente no se logró acceder al herbario de la Universidad de El Salvador (ITIC).

HYGROPHILA COSTATA Nees & T. Nees, Pl. Hort. Bonn. Icon. 2: 7, t. 3. 1824.

Sinónimos: *Hygrophila conferta* Nees; *H. guianensis* Nees; *H. lacustris* (Schltdl. & Cham.) Nees

Hierba acuática emergente, de hasta 1.5 m de alto; tallos cuadrangulares, glabros que enraízan en los nudos inferiores. Hojas lanceoladas a elípticas, de hasta 15 cm de largo y 1 cm de ancho, ápice acuminado, base atenuada, márgenes enteros a undulados, haz glabra, envés escasamente con pelos en los nervios; pecíolos hasta 3 cm de largo, glabros. Inflorescencias axilares en fascículos de 3–4 flores, sésiles; brácteas lanceoladas, de hasta 9 mm de largo y 3 mm de ancho; sépalos 5, iguales, lineares, 5–9 mm de largo en la antesis y de 6–12 mm de largo en fruto; corola bilabiada, 5–9 mm de largo, blanca, labio superior 2-lobado, el inferior 3-lobado; frutos sésiles, angostamente oblongos, 8–13 mm de largo, glabros. Fig. 1.

Distribución y hábitat. Estados Unidos a Argentina. En El Salvador se encuentra a lo largo de los riachuelos en bosque tropical semideciduo mixto submontano, en suelos bien drenado de cenizas volcánicas (MARN 2011), a una elevación de 1040 m.s.n.m. Fig. 2.

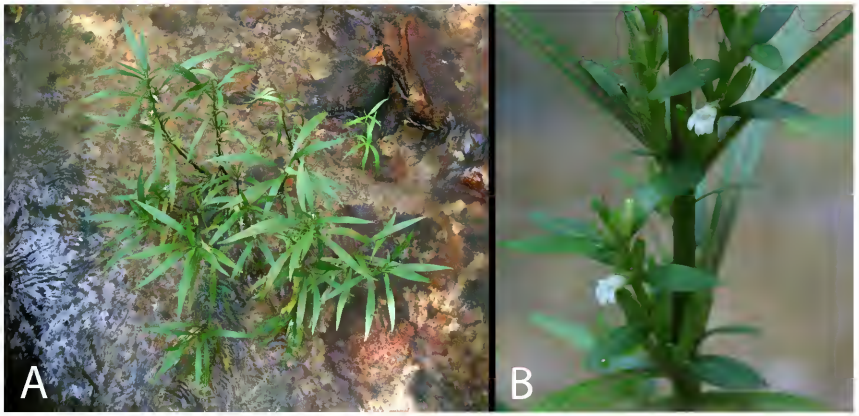

Figura 1. *Hygrophila costata* (*Rodríguez & Galán 04358*). A. Hábitat. B. Flores y frutos.

Figura 2. Sitio de recolección de *Hygrophila costata* en El Salvador.

Discusión. Aunque la distribución de la especie es amplia (Estados Unidos a Argentina), la especie es poco frecuente de encontrarse en El Salvador a comparación de los países vecinos en la región Centroamericana como Guatemala, Honduras, y Nicaragua (Durkee 2001; Daniel 2005, 2010). Esta especie ocurre generalmente en hábitats húmedos, y se ha utilizado como un indicador de los humedales en porciones de su distribución (por ejemplo, Lichvar 2013).

Material examinado. **EL SALVADOR**. **Morazán**. Municipio de Joateca, Caserío El Tizate, A.N.P. La Ermita, alrededores de La Fuente, Terreno El Garrobo de ASAPSMA (Asociación Administradora de Agua Potable, Saneamiento y Medio Ambiente), 13° 56′ 23′′ N y 88° 04′ 18′′ W, 9 Oct 2013 (flr, frt), *D. Rodríguez & P. Galán 04358* (CAS, LAGU).

AGRADECIMIENTOS

Agradezco al personal del Herbario MHES por la amabilidad en la búsqueda de la especie en sus colecciones.

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TAXONOMY OF *ERYTHRANTHE SECT. ERYTHRANTHE* (PHRYMACEAE)

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ABSTRACT

Erythranthe sect. *Erythranthe* includes nine species: *E. cardinalis*, *E. cinnabarina*, *E. flammea*, *E. eastwoodiae*, *E. erubescens*, *E. lewisii*, *E. parishii*, *E. rupestris*, and *E. verbenacea*. **Erythranthe cinnabarina** Nesom, **sp. nov.**, includes the populations previously identified as *E. cardinalis* from three counties in southeastern Arizona — and is the phyletic sister of *E. cardinalis*. **Erythranthe erubescens** Nesom, **sp. nov.**, includes populations of the pink-flowered, Sierran race previously included within *E. lewisii* — and is the phyletic sister of *E. lewisii*. *Erythranthe lewisii* is narrowed in concept to the northern, magenta-rose-flowered race. **Erythranthe flammea** Nesom, **sp. nov.**, includes plants previously identified as *Mimulus nelsonii*, except for the type of *M. nelsonii*, which was a collection of the earlier-named *Mimulus verbenaceus*. Very rarely has such a complete array of evidence (geographic, ecological, morphological, genetic, phylogenetic) been available for the description of new species. A key to the species and a typification summary, morphological description, ecological summary, and county-level (in the USA) distribution map for each species are provided. A lectotype is selected for *E. rosea*, which is a synonym of *E. lewisii*.

The establishment of *Erythranthe* as a genus (Spach 1840) included only the type species, *E. cardinalis*. Greene (1885) reduced *Erythranthe* to a section of *Mimulus* and included *M. cardinalis*, *M. lewisii*, and *M. parishii*, but Grant's sect. *Erythranthe* (1924) included only the red-flowered species *E. cardinalis*, *E. verbenacea*, *E. rupestris*, and *E. nelsonii* — placing *E. lewisii* and *E. parishii* together in her broadly conceived sect. *Paradanthus*. Pennell (1951) included *E. cardinalis* and *E. lewisii* in sect. *Erythranthe*, placing *E. parishii* among the species of sect. *Paradanthus*. Pollen morphology of sect. *Erythranthe* is closely similar to that of the rest of the genus (Argue 1980), except for sect. *Simiola*. Molecular studies by Beardsley et al. (2003, 2004), however, securely establish the identity of sect. *Erythranthe* as a distinct group, including *E. parishii*, and its phyletic position within the genus and provide a well-documented hypothesis of relationships among the species (Fig. 1).

Attempted crosses between *Erythranthe cardinalis* and *E. lewisii* and various species of other *Erythranthe* sections (sects. *Mimulasia*, *Mimulosma*, *Monantha*, *Simiola*) as well as *Mimulus ringens* (*Mimulus* sensu stricto) were unsuccessful in producing progeny (Vickery 1966; Heisey et al. 1971).

Cytogenetic studies of sect. *Erythranthe* emphasizing crossing experiments were done by Carnegie researchers (Nobs & Heisey 1964, 1965; Heisey et al. 1971); these were largely repeated by Vickery (Vickery & Anderson 1967; Vickery 1978). Two main species groups were apparent through the crossing relationships — *M. lewisii* and *M. cardinalis* and the more eastern-distributed group of *M. eastwoodiae*, *M. verbenaceus*, *M. nelsonii*, and *M. rupestris* (the latter not included in the crossing experiments) — molecular analyses found that these groups constitute phylogenetic sisters.

The taxa of sect. *Erythranthe* are fewer and more unambiguously defined than those of sect. *Simiola*, yet taxonomic problems have remained. Especially significant have been the interpretation of the two morpho-geographic races of *E. lewisii* and of the long-disjunct populations in southeastern Arizona identified as *E. cardinalis*. Generalized distribution maps of the entities have been presented (e.g., Heisey et al. 1971; Vickery & Wullstein 1987; Beardsley et al. 2003) but the only formal taxonomic treatment of the whole group has remained that of Grant (1924).

The outline of taxonomy presented here is largely in agreement with that of Heisey et al (1971) and Beardsley et al (2003), except for the addition of two species in a reconsideration of the taxonomic status of the 'northern' (widespread, typical) and 'Sierra Nevada' (mostly California endemic) races of *E. lewisii* and the relationship between typical *E. cardinalis* and the populations from southeastern Arizona heretofore identified as *E. cardinalis*. The present study also clarifies issues of typification, provides morphological descriptions, clarifies the geographical distributions of *E. eastwoodiae* and *E. verbenacea*, confirms the distinction of *E. verbenacea*, and provides a name for the Mexican plants previously identified as *Mimulus nelsonii*.

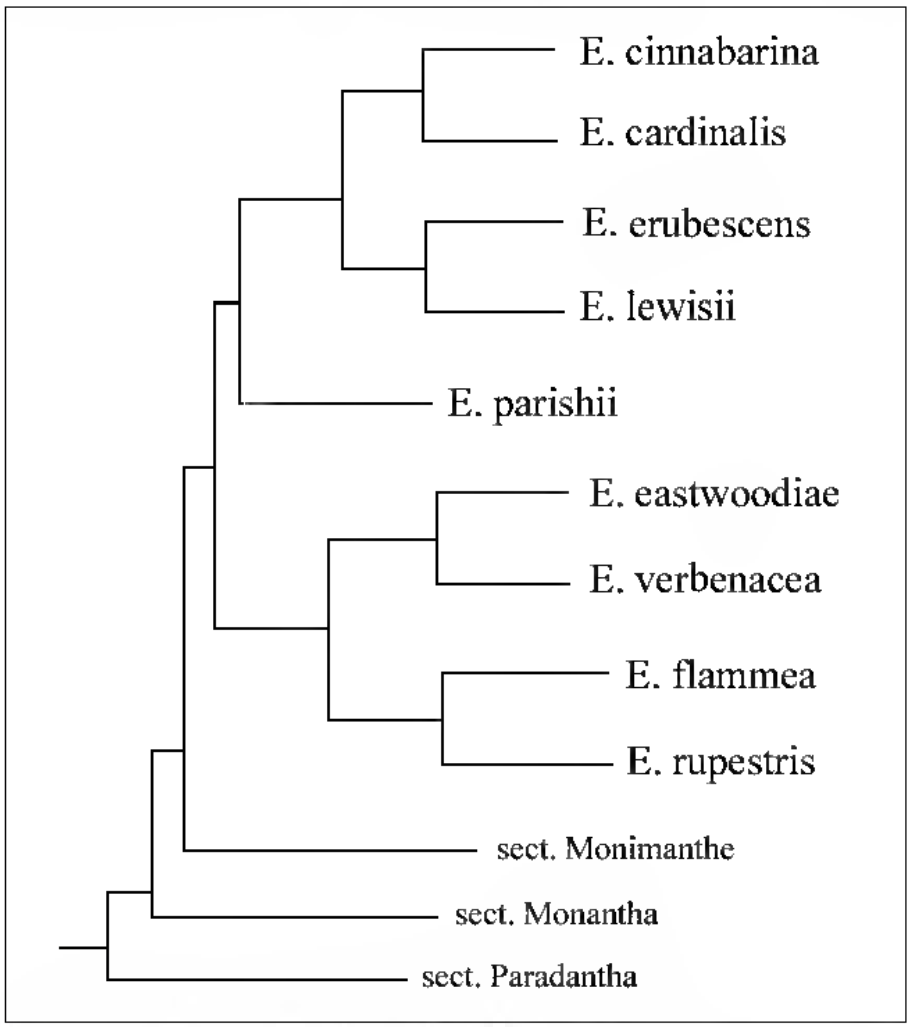
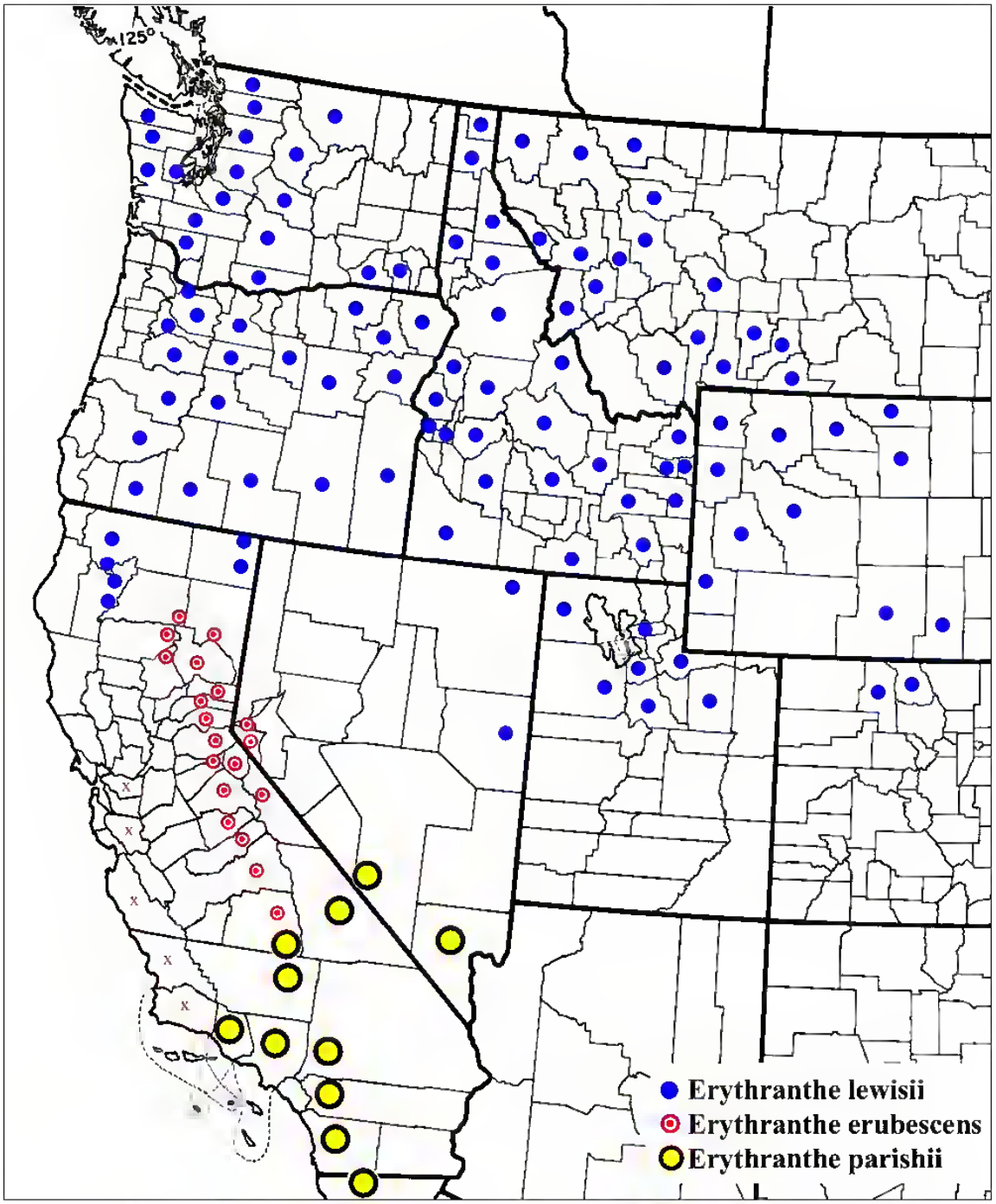
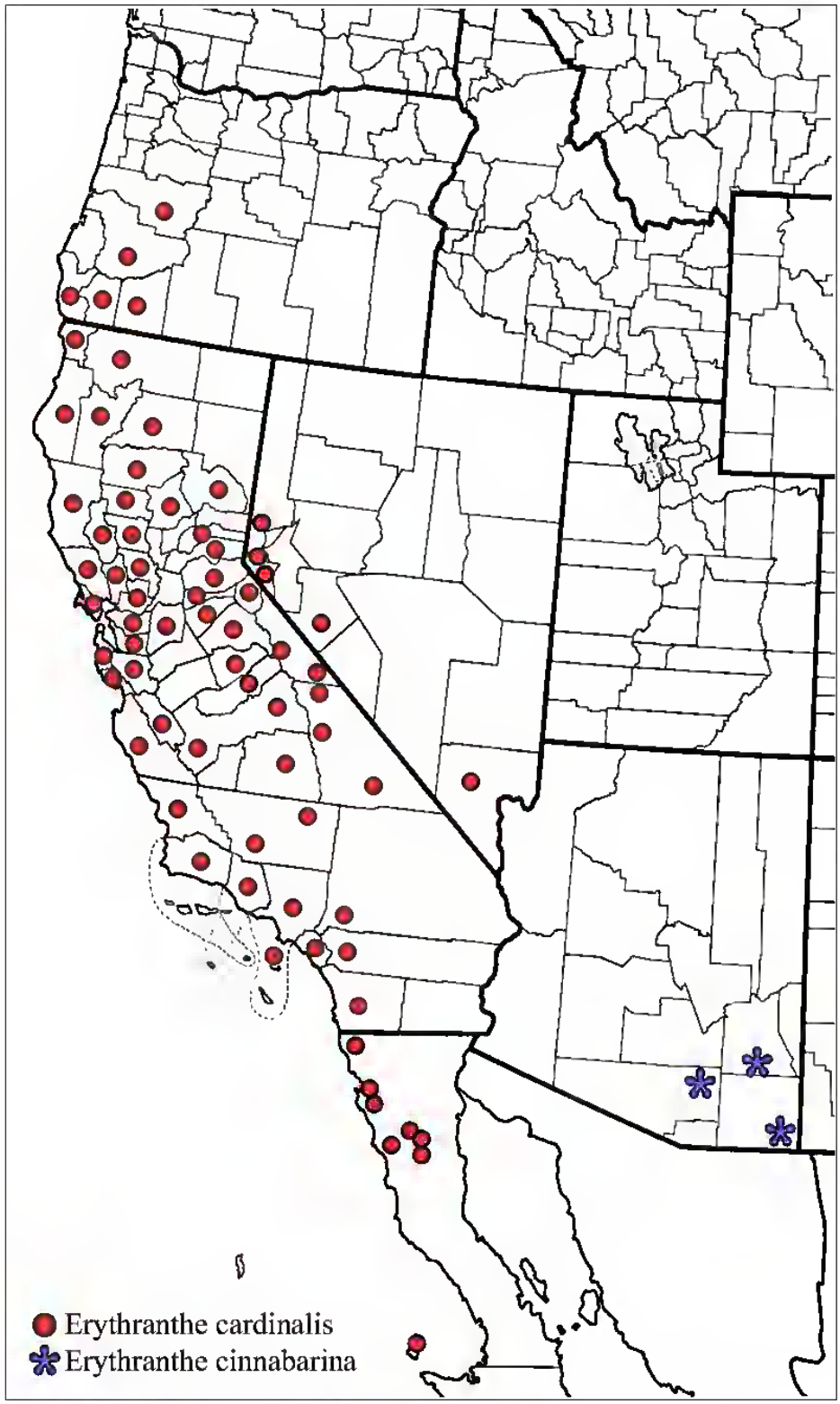


Figure 1. Phylogenetic relationships within and immediately outside of sect. *Erythranthe*, as indicated by Figures 2, 3, and 4 of Beardsley et al. (2003) and Figure 2 of Beardsley et al. (2004). Also see the summary in Figure 1 of Barker et al. (2012). Species added to sect. *Erythranthe* in the current study are *E. erubescens* and *E. cinnabarina*. *Erythranthe flammea* is the name of plants previously identified as *Mimulus nelsonii*, which is a synonym of *E. verbenacea*.

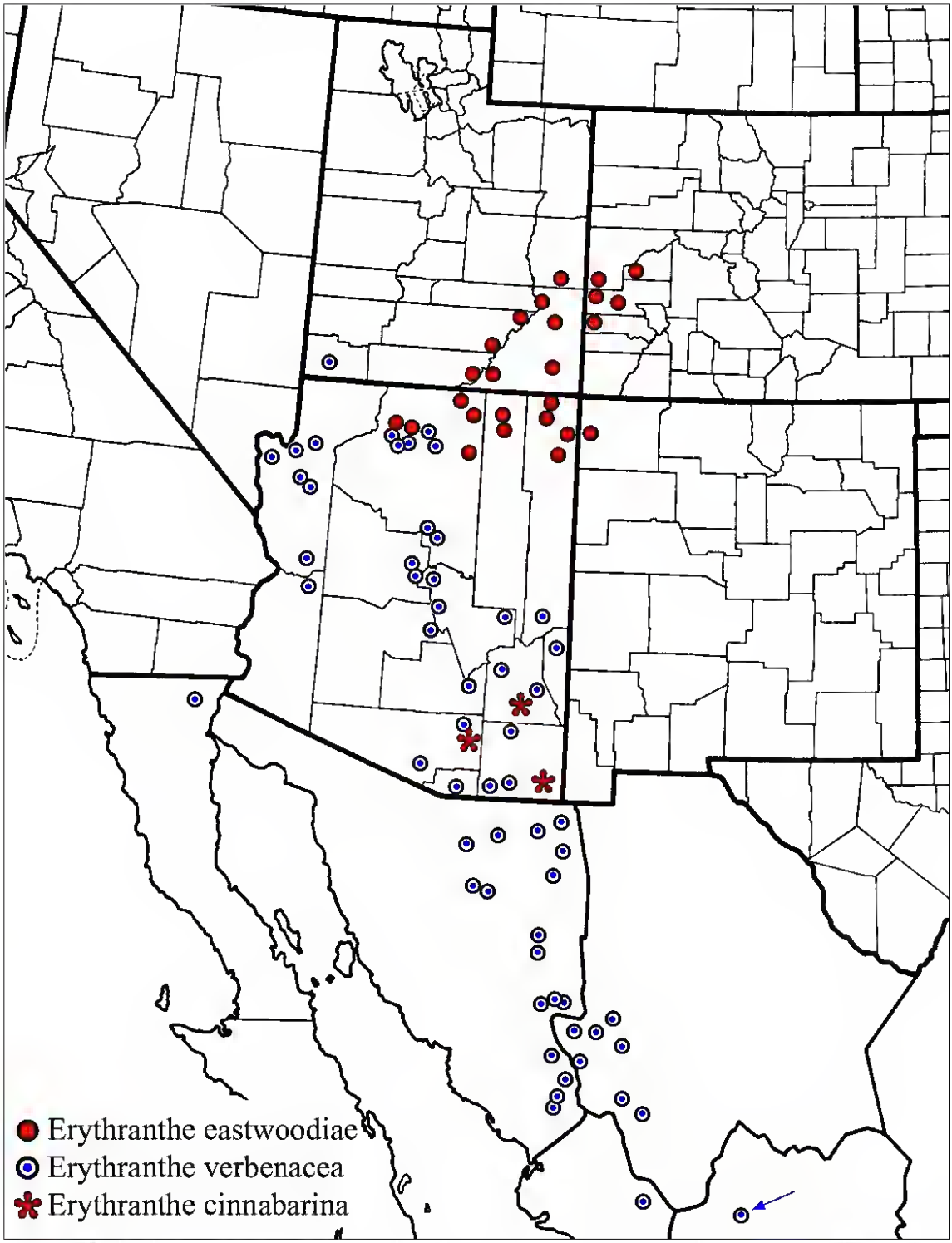
Formal nomenclature for *Erythranthe* and rationale for its separation (as a genus of more than 100 species) from *Mimulus* L. sensu stricto were presented by Barker et al. (2012). Previous detailed taxonomic studies of species groups at sectional rank within the genus have dealt with sect. *Achlyopitheca*, sect. *Mimulosma*, and sect. *Simiola* (Nesom 2012a, 2012b, 2012c).



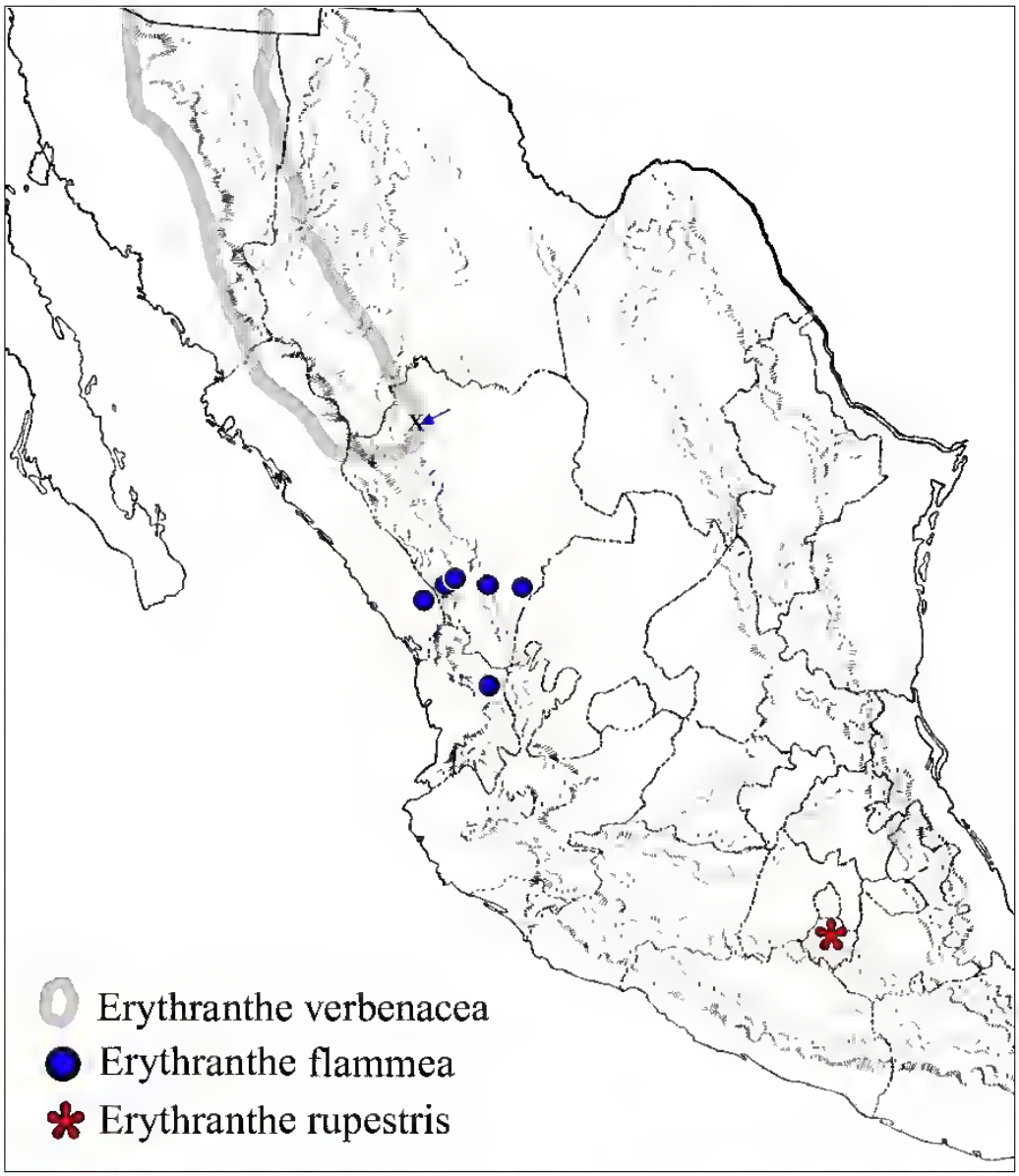
Map 1. Distribution of *Erythranthe lewisii*, *E. erubescens*, and *E. parishii*. The distribution of *E. lewisii* continues through southwestern Alberta and British Columbia into southern Alaska (see E-Flora BC 2013). The range of *E. parishii* extends slightly further southward into the Sierra San Pedro Martir of Baja California. Symbols in California and Nevada are placed within counties corresponding to the location of the populations, thus the portrayal of disjunction in northern California between *E. erubescens* and *E. lewisii* is accurate. "X"s show counties considered by Rogers (2010) as California coast range localities where David Douglas might have collected *Mimulus roseus* (within the area explored by Douglas in 1831-32) — Rogers concluded that the *M. roseus* type probably was from Santa Barbara County.



Map 2 Distribution of *Erythranthe cardinalis* and *E. cinnabarina*. Placement of symbols in larger counties indicates actual position of population systems.



Map 3. Distribution of *Erythranthe eastwoodiae*, *E. verbenacea*, and *E. cinnabarina*. Some localities for *E. eastwoodiae* are from DAVP-Utah (2014), COLO-Database (2014), and SEINET (2014). Collections documenting the disjunct population system of *E. verbenacea* in Baja California are cited in the text. The arrow points to the type locality of *Mimulus nelsonii*



Map 4. Distribution of *Erythranthe flammea* and *E. rupestris*. Arrow points to type locality of *Mimulus nelsonii*, at the southern extremity of the range of *E. verbenacea* (shown in outline)

Species concepts and evolutionary overview

The population system from south-central Durango previously identified as *Mimulus nelsonii* (here as *Erythranthe flammea*) has been accepted in previous studies as a distinctive species. The present study more accurately represents its geography and morphology and provides an epithet, since the type of *M. nelsonii* is a plant of the earlier-named *M. verbenaceus*.

The formal description here of *Erythranthe erubescens* and *E. cinnabarina* provides a fuller and more accurate understanding of the evolutionary history of sect. *Erythranthe*. Both taxa previously have been recognized and discussed as unnamed variants within *E. lewisii* and *E. cardinalis*, respectively, but both deserve specific rank with justification equalling the other species of the section.

Species as recognized in sect. *Erythranthe*, as in 99% of other accepted species of vascular plants, are first "morphological (or morpho-geographic) species." The taxa of sect. *Erythranthe*, though, are remarkable in having been the subject of detailed experimental studies of their genetics and reproductive isolation (only *E. rupestris* has not been included in experiments), and thus, for the most part, can also be recognized as "biological species" in the sense of Mayr.

Geography enforces reproductive isolation between the sisters *Erythranthe erubescens* & *E. lewisii* and postzygotic isolation mechanisms (as documented) also are in effect. Differences in corolla color and shape between E. *erubescens* and *E. lewisii* may reflect the influence during speciation of selective pressure from pollinator preference. Primary pollinators of *E. erubescens* are the bumblebees *Bombus balteatus*, *B. centralis*, and *B. flavifrons*, and *B. vosnesenskii* (e.g., Heisey et al. 1971; Schemske & Bradshaw 1999) — *B. flavifrons* and *B. vosnesenskii* occur in the California Sierra Nevada and also in western Oregon where *E. lewisii* is sympatric with *E. cardinalis*; *Bombus balteatus* and *B. centralis* occur in the California Sierra Nevada but not in western Oregon (Koch et al. 2012), at least suggesting possibilities of pollinator-mediated selection.

Distinctions between the sisters *Erythranthe cardinalis* & *E. cinnabarina* probably evolved in allopatry, in view of their present wide disjunction. Experimental studies show that they are postzygotically isolated, but apart from their allopatry, possible prezygotic mechanisms have not been investigated. Primary pollinators of *E. cardinalis*, the hummingbirds *Calypte anna* and *Selasphorus rufus* (e.g., Heisey et al. 1971; Schemske & Bradshaw 1999), also occur in the range of *E. cinnabarina* (Cornell Lab of Ornithology 2014). Although the populations of *E. cinnabarina* occur in three geographically discrete and isolated systems, ecological and morphological variability within the species appears to be relatively narrow.

Only three species of sect. *Erythranthe* do not occur in sympatry with any other species — *E. eastwoodiae* (allopatric or perhaps parapatric with its sister *E. verbenacea*) and the sister pair E. *flammea* and *E. rupestris* — thus there is no natural test of their reproductive isolation. The geographic range of *E. cinnabarina* is mostly within that of *E. verbenacea* — the two are ecologically isolated and apparently rarely come into contact, but they are not sister species thus their sympatry does not provide an assessment of the development of reproductive isolation during speciation. *Erythranthe parishii* is parapatric with *E. cardinalis* in a small area of Tulare County where their ranges are contiguous (Fishman et al. 2013) — hybrids are formed where they come into contact (Paul Beardsley, pers. comm. 2014).

The geographic range of *Erythranthe cardinalis* completely encompasses that of *E. erubescens*. At the northern extension of its range (northwestern California and southwestern Oregon), *E. cardinalis* is sympatric with *E. lewisii*. Pollinator preference presumably plays a major role in isolating *E. cardinalis* and *E. lewisii* where they are sympatric, as it does with *E. cardinalis* and *E. erubescens*, but potential ecological distinctions (elevation, phenology) between *E. cardinalis* and *E. lewisii* have not been investigated.

In the molecular analysis of Beardsley et al. 2003), *Erythranthe cardinalis* and *E. lewisii* were interpreted to be sister species and that interpretation has been followed in subsequent studies (e.g., Ramsey et al. 2003; Angert & Schemske 2005; Angert et al. 2008; Fishman et al. 2013). In context of the species added in the present review, the phylogeny indicates that differentiation of hummingbird-pollination morphology preceded the speciation events that produced the two pairs of sister species — *E. lewisii* & *E. erubescens* and *E. cardinalis* & *E. cinnabarina*.

ERYTHRANTHE sect. **ERYTHRANTHE**

Erythranthe Spach, Hist. Nat. Veg. Phan. 9: 312. 1840. *Mimulus* sect. *Erythranthe* (Spach) Greene, Bull. Calif. Acad. Sci. 1: 108. 1885. **TYPE**: *Erythranthe cardinalis* (Dougl. ex Benth.) Spach, the only species in the protologue.

Perennial or (*E. parishii*) annual herbs, stems and leaves glabrous to puberulent or hirsute, usually glandular; leaf blades oblong or elliptic to oblanceolate, or narrowly lanceolate, shallowly toothed, palmately veined (3–5-nerved from the base); fruiting pedicels longer than calyces; calyces with sharp, definite angles and flat sides, lobes usually equal to subequal, usually apically caudate; corollas deciduous, relatively large (tube-throat 8–42 mm long), strongly red to purplish, magenta-rose, pink, or white, rarely yellow, limbs bilabiate, throat open, lobes shallowly notched to slightly retuse or entire, spreading to sharply reflexed; anther thecae white-villous (glabrous in E. parishii. x = 8.

Mexico

1. Stems prostrate with leafy stolons, cliff faces; Morelos ..... 9. **Erythranthe rupestris**
1. Stems erect, without stolons; Durango to the north and northwest.

2. Corolla tube-throats infundibular, exserted 2–11 mm beyond calyx margin; anther thecae spreading (non-reflexed); Baja California ..... 4. **Erythranthe cardinalis**
2. Corolla tube-throats tubular, exserted 13–25 mm beyond calyx margin; anther thecae reflexed.

3. Leaf blades elliptic to obovate, rhombic-ovate, or broadly spatulate, 50–75 mm x 15–26(–30) mm; corolla tube-throats 25–35 mm; calyx lobes ovate with a linear-triangular apex ..... 6. **Erythranthe verbenacea**
3. Leaf blades narrowly lanceolate, 60–95 mm x 7–15(–20) mm; corolla tube-throats 40–45 mm; calyx lobes narrowly triangular with a linear apex .....8. **Erythranthe flammea**

USA

1. Taprooted or fibrous-rooted, annual; fruiting pedicels 9–24 mm; corolla tube-throats 8–10 mm ..... 1. **Erythranthe parishii**
1. Rhizomatous and/or stoloniferous, perennial; fruiting pedicels (25–)30–95 mm (10–30(–40) mm in *E. eastwoodiae*); corolla tube-throats (15–)20–36 mm.

2. Corollas mostly light pink or magenta-rose to rose-purple or pink-purple; dorsal petals mostly free; anthers and stigma included; leaf margins denticulate to subentire or entire.

3. Corollas mostly magenta-rose, rose-purple, or pink-purple; calyx tube 12–15(–17) x 9–12 mm (pressed); widespread in northwestern USA ..... 2. **Erythranthe lewisii**
3. Corollas usually light pink; calyx tube 14–19 x 6–8 mm (pressed); Sierra Nevada of California ..... 3. **Erythranthe erubescens**

2. Corollas orange–red to scarlet or crimson; dorsal petals fused for most of length, erect; anthers and stigma exserted; leaf margins dentate to serrate.

4. Stems prostrate with leafy stolons; fruiting pedicels 10–30(–40) mm ..... 7. **Erythranthe eastwoodiae**
4. Stems erect to decumbent, rhizomatous but without stolons; fruiting pedicels (25–)50–120 (very rarely to 150) mm.

5. Corolla tube-throats tubular, exserted 13–25 mm beyond calyx margin; anther thecae reflexed ..... 6. **Erythranthe verbenacea**
5. Corolla tube-throats infundibular, exserted 2–11 mm beyond calyx margin; anther thecae spreading (non-reflexed).

6. Leaves adaxially glandular-villous on veins and lamina; calyx 17–28(–30) mm, lobes 4–7 mm, ovate to ovate-deltate, lobes apically attenuate-acute, not caudate; corolla tube-throat (15–)20–30 mm; California, Oregon, Baja California, 50–2300(–2800) m ..... 4. **Erythranthe cardinalis**
6. Leaves adaxially glabrous to minutely sessile- or stipitate-glandular; calyx (27–)29–34 mm, lobes 7–10 mm, ovate, abruptly attenuate to a linear-caudate apex; corolla tube-throat 29–36 mm; Arizona, 2100–3300 m ..... 5. **Erythranthe cinnabarina**

1. **ERYTHRANTHE PARISHII** (Greene) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. *Mimulus parishii* Greene, Bull. Calif. Acad. Sci. 1: 108. 1885. **TYPE: USA. California.** [San Bernadino Co.]: Cox Ranch, Mohave River, Aug 1882, *S.B. Parish & W.F. Parish 1465* (duplicates: F?, GH digital image!, M digital image!, PH 2 sheets digital images!, UC, US?, DS digital image!). On the handwritten label of the DS sheet, "Cox' Ranch" is crossed through and replaced by "Rock Spring." The GH sheet has "Bear Valley, San B. Mts., Aug 1882" but like the others, it is numbered *Parish & Parish 1465*.

In the protologue Greene cited: "On the Mohave slope of the San Bernadino Mountains, at Cox's Ranch, N side of San Bernadino Mts., Aug 1882, Parish Bros. No. 1465. Collected again in the summer of 1884, by the Rev. J.C. Nevin, and Mr. J.C. Oliver, in Los Angeles County, and by Mr. C.R. Orcutt, on the peninsula of Lower California in September of the same year." Grant (1924) cited the Parish collection as the "type" but did not distinguish among the duplicates (she cited "U.S., F, Calif., and Stanford, *type collection*"). Presumably the US specimen was the one that Greene had at hand in his description and would be the best choice for lectotype, but the species is not currently listed in the US type database (nor in the F type database).

Annual herbs, taprooted or fibrous-rooted. **Stems** erect, (3–)10–85 cm, mostly simple. **Herbage** villous-glandular to stipitate-glandular. **Leaves** cauline; blades oblanceolate to narrowly ovate or oblong, (8–)15–75 mm x 3–17 mm, palmately 3-veined, thin, apex acute to obtuse, base slightly narrowed, subclasping to clasping, margins distally denticulate to irregularly dentate; petioles absent. **Flowers** ca. 4–12, from medial to distal nodes. **Fruiting pedicels** 9–24 mm, ascending-erect. **Calyx** fruiting cylindric-campanulate, 8–13 mm, not inflated, slightly ridge-angled, villous-glandular to short stipitate-glandular, lobes subequal, 1–2 mm, deltate-apiculate, erect, glandular-ciliate. **Corollas** white to light lavender, pinkish, or rosy, palate ridges yellow, with or without small reddish spots on the palate and lower lip, tube-throats cylindric, 8–10 mm, exserted 1–3 mm beyond calyx, weakly bilabiate, lobe apices truncate to rounded, slightly erose, throats open. **Styles** glabrous. **Anthers** included, thecae spreading, glabrous. **Herkogamous** (weakly, stigma sometimes at essentially same level as upper pair of stamens). **Capsule** included, ellipsoid, slightly beaked, 6–10 mm. $2n = 16$ (as inferred from Fishman et al. 2013).

Flowering May–Aug. Wet, sandy streamsides, rocky riverbeds, canyon drainages; 400–2300 m; Calif., Nev.; Mexico (Baja California). Map 1.

In the molecular studies by Beardsley et al. (2003, 2004), *Erythranthe parishii* is sister to *E. cardinalis*/*E. cinnabarina*-*E. lewisii*/*E. erubescens*. Its annual duration, which is unique in the section, is derived from perennial ancestry. According to Fishman et al. (2013), *E. parishii* often co-occurs with *E. cardinalis* where their ranges are contiguous, presumably in Tulare County. Documentation of the presence of *E. parishii* in Nevada is in Lloyd and Mitchell (1973).

2. **ERYTHRANTHE LEWISII** (Pursh) Nesom & Fraga, Phytoneuron 2012-39: 36. 2012. *Mimulus lewisii* Pursh, Fl. Amer. Sept. 2: 427, plate 20. 1814 [1813]. **LECTOTYPE** (Reveal et al. 1999, p. 33): **USA. [Montana.]** Plate 20 (reproduced here as Fig. 2), Fl. Amer. Sept. 2: 427. 1814 [1813]. Protologue: "On the head springs of the Missouri, at the foot of Portage hill," 1805, *M. Lewis s.n.*

The Lewis collection was noted by Pursh to have been seen in the Lewis herbarium ("v.s in Herb. Lewis nec non Lambert"), but no type material is now known to be extant (see Reveal et al. 1999), thus the protologue illustration becomes the lectotype. The type probably was collected either in the Great Falls area in Cascade Co., Montana, sometime from 21 Jun-14 Jul 1805 (as implied by the reference to "Portage Hill") or more likely along Trail Creek toward Lemhi Pass in Beaverhead Co., Montana, on 12 Aug 1805 (as implied by the reference to the "headsprings of the Missouri") (Reveal et al. 1999, UMDANSP 2008).

Mimulus roseus Dougl. ex Lindl., Edwards's Bot. Reg. 19 [n. ser., 6]: 1591, pl. 1591. 1 June 1833. **LECTOTYPE** (designated here): **USA. Oregon or Washington**. Plate 1591 (reproduced here as Fig. 6), Bot. Reg. 19: 1591. 1833. **The illustrated plant was cultivated in London by the Horticultural Society from seeds sent by** *David Douglas* **(*s.n.*).**

Lindley noted this in the 1833 Botanical Register protologue: "This beautiful Monkey-flower was sent by Mr. Douglas from Northern California in 1831. In his letter to the Horticultural Society he spoke of it as extremely rare, and the most striking object he had met with in that country. A very few grains of seed were all that reached England, and from those a small number of plants were obtained, one of which is now represented. ... Only a very small quantity of seed was saved last year, by means of which it has been preserved. ... It flowers in July and August."

Mimulus roseus previously has been treated as a synonym of a broadly construed *M. lewisii* (e.g., Hooker 1840, followed by Bentham 1846, Gray 1888, and Grant 1924) or else the name has not been considered even as a synonym (e.g., Greene 1885; Pennell 1951). With recognition here that the pink-flowered Sierra Nevadan plants of California constitute a species (*Erythranthe erubescens*, see below) distinct from typical, magenta-rose-flowered *E. lewisii*, the name *M. roseus* might be considered as the name for the Sierran plants, especially as Rogers (2010) accepted the protologue statement regarding California provenance and concluded that Douglas probably made the collection in Santa Barbara County, although it is outside of the currently known range of the species. Douglas collected in California in 1831 and 1832 but never reached the area where the Sierran race occurs (Map 1).

In addition to the protologue illustration (Fig. 6), three more of *Mimulus roseus* also were quickly published (Hooker 1834, Loddiges 1835, Don 1835, reproduced here as Figs. 7, 8, and 9, respectively) of plants probably from seeds immediately derived from the originally germinated plants. All four of the illustrations unequivocally show the magenta-rose corollas of typical *E. lewisii* — not the light pink of the California Sierran race. In contrast to Rogers's interpretation, it is thus reasoned here that Douglas collected the seeds of *M. roseus* in the Cascade Mountains close to the Columbia River or in the Blue Mountains east of Walla Walla, Washington, where he traveled through the range of *M. roseus* in July of 1830. On 11 October 1830, he shipped 3 chests of seeds (perhaps including *M. roseus*), but without dried plants, to London from the mouth of the Columbia river (fide Hooker 1836). The *Mimulus roseus* protologue was published 1 June 1833, thus it would have taken a little more than two years (ca. 31 months) for the seeds to travel to Europe, be received, reach the hands of horticulturalists and be grown to maturity, and then the illustration prepared. I have not seen the letter mentioned by Lindley (from Douglas to the Horticultural Society) or any reference to it.

This assumes that Lindley's comment that the seeds were received from Douglas in California in 1831 was mistaken (perhaps a clerical error in handling or labeling the seeds) or else that Douglas sent Oregon-collected seeds from California. If the latter proved to be correct, it would imply that Douglas took the seeds with him from the Columbia River to California and

shipped them from there to London in 1831. In a letter to W.J. Hooker (23 Nov 1831, from Monterey), Douglas wrote that "This, with many others, I trust you may yet have the pleasure of describing from living specimens, as I have sent to London upwards of one hundred and fifty nondescript plants, which I hope will bloom next season." Presumably these were California plants with bulbs or rhizomes or represented by cuttings, and according to the letter mentioned by Lindley in the protologue, Douglas did not consider *Mimulus roseus* to be "nondescript." Douglas later (23 October 1832, from the Columbia River, Oregon) wrote Hooker that he shipped "the whole of his California collection" — apparently referring to his dried specimens — from Hawaii on 8 September 1832.

Summarizing his California collections in the 23 Nov 1831 letter to Hooker, Douglas noted that "... to *Mimulus* I have also added several, among them the magnificent *M. cardinalis*, an annual, three or four feet high, handsomer than *M. luteus*." He had not earlier mentioned *M. luteus*, so it seems he assumed that *M. luteus* already would have reached England and been known — prior to the shipment of his California collections.

An undated specimen identified as *Mimulus lewisii*, with label data of "Oregon Douglas," is at GH (digital image!), the label is "Herb. A. Gray" on characteristic blue paper and the data are in Asa Gray's handwriting. Presumably Gray obtained this in 1838-39 on his first European trip. The preface of A Flora of North America (Torrey & Gray 1838, p. viii) noted that "We are under deep obligations to Mr. Bentham ... especially for a very full set of the plants collected by the late Mr. Douglas in Oregon and California, which were confided to him, as Secretary of the London Horticultural Society, for distribution." Bentham's reference (Scrophularineae Indicae, 1835) in the description of *M. roseus* to "Ad Columbia flumen, *Douglas*" surely alluded to this collection. None of Douglas's accounts mentions an encounter with *M. lewisii* on his first trip to the Pacific Northwest, thus this collection probably was made on the second trip. It was not, however, in the original material seen by Lindley.

The undated specimen at M (Fig. 2) was distributed with a printed label by the Horticultural Society of London and, although "D. Douglas" might be taken as the collector (as implied by the label), the plant probably was grown in London from seed, either from the original seed collection by Douglas or from descendants of the original cultivars.

Mimulus roseus var. *glabrior* Hook., Fl. Bor. Amer. 2: 100. 1840. **TYPE: CANADA. Alberta.** Protologue: "Mountains N of the Smoking River (*Drummond*); apparently very rare, or too early for the blossoming, for there are only two specimens in the collection, and only one in flower; and these are more glabrous than Mr. Douglas's specimens, which, as far as I know, were all gathered in California.—I think the *M. lewisii*, Ph. is probably a dwarf state of this species." (holotype: K? or E?). Thomas Drummond was in British Columbia on the Smoky River of west-central Alberta in August and September, 1826 (Geiser 1937).

Mimulus lewisii var. *exsertus* Coult. & Fisher, Bot. Gaz. 18: 302. 1893. **TYPE: USA. Colorado.** High mountains of northern Colorado, 1892, *G.E. Osterhout s.n.* (holotype: F digital image!).

Mimulus lewisii var. *tetonensis* A. Nels., Bot. Gaz. 34: 31. 1902. *Mimulus lewisii* forma *tetonensis* (A. Nels.) Macbr. & Pays., Contr. Gray Herb. 49: 67. 1917. **TYPE: USA. Wyoming.** Summit of Tetons above Lee's Lake, 11,000 ft, 26 Jul 1901, *E.D. Merrill & E.N. Wilcox 1072* (holotype: RM; isotype: NY digital image!).

Mimulus lewisii var. *alba* J.K. Henry, Fl. S. Brit. Columbia, 268. 1915. *Mimulus lewisii* forma *alba* (J.K. Henry) B. Boivin, Naturaliste Canad. 93: 1061. 1966 [published 1967]. **TYPE: CANADA. British Columbia.** As cited in the protologue: "With the species, Mt. Cheam; Crown Mt., North Vancouver." Specimens not located.

Perennial herbs, rhizomatous, sometimes described as having a musky odor. **Stems** erect, (15–)25–60(–75) cm, mostly simple. **Herbage** stipitate-glandular to glandular–villous, viscid. **Leaves** cauline; blades elliptic to ovate, ovate-lanceolate, or broadly lanceolate, (10–)25–75(–90) mm x 5–35 mm, 3–5-palmately veined from the base, margins denticulate with 2–5 pairs of teeth to subentire or entire, apex acute, base rounded or cuneate, subclasping; petioles absent. **Flowers** 2–6(–

10), axillary at leafy medial to distal nodes. **Fruiting** pedicels (25–)35–70 mm. **Calyx** broadly cylindric-campanulate, 15–22 mm, not inflated, stipitate-glandular to glandular–villous, lobes subequal, 3–5(–7) mm, deltate-triangular with caudate apices, erect, not ciliate. **Corollas** mostly rose-pink or magenta-rose to pink-purple or reddish purple, rarely crimson or pale violet, tube-throats infundibular, 22–28 mm, exserted 6–12 mm from the calyx, strongly bilabiate, lobe apices usually truncate to shallow convex and shallowly retuse, throats open. **Styles** 25–28 mm, glabrous. **Anthers** included, thecae spreading, white-villous. **Herkogamous**. **Capsule** included, cylindroid, 6–11 mm. $2n = 16$ (Vickery et al. 1958, 1963, 1986; Nobs & Heisey 1965; Heisey et al. 1971).

Corolla color has been described as violet-red, rose-purple, rose, magenta, magenta-red, crimson, deep rose with orange spots on lip, reddish pink, pink-purple. Exceptions: "pinkish-white" in Yakima/ Skamania Co., Washington (Mt. Paddo, *Suksdorf 5779*, MO); "white or tinged with yellow," in Teton Co., Wyoming (as described in the protologue of *Mimulus lewisii* var. *tetonensis*). The type was described by Pursh as having a "beautiful pale purple" corolla with dark lines. White-flowered mutants occur sporadically (e.g., Wu et al. 2013, and see *M. lewisii* var. *alba*).

Flowering Jun–Sep. Stream banks, gravel bars, around springs, wet meadows, boggy areas, ditches, subalpine slopes, alpine meadows, wet talus, crevices; (1800–)2200–9500(–10,600) ft; Alta., B.C.; s Alaska, Idaho, Mont., Nev., Oreg., Utah, Wash., Wyo. Map 1.

Rationale for segregation of the Sierra Nevadan 'race' of *Erythranthe lewisii* as a distinct species is provided under *E. erubescens*.

3. ERYTHRANTHE ERUBESCENS Nesom, **sp. nov.** **TYPE**: **USA. California**. Nevada Co.: Ridge above Donner Pass, 7500 ft, 10 Aug 1903, *A.A. Heller 7141* (holotype: MO!; isotype: MO!).

Similar to typical *Erythanthe lewisii* but distinct in its light pink corollas (vs. mostly magenta-rose to purplish), more broadly cylindric calyx tubes (14–19 x 6–8 mm vs. 12–15(–17) x 9–12 mm), and its geographic range in the Sierra Nevada of California (vs. widespread from southern Alaska south to northern California, northern Utah, and northern Colorado. Genetically isolated and phylogenetically distinct from typical *E. lewisii*.

Perennial herbs, rhizomatous. **Stems** erect, 25–90 cm, mostly simple. **Herbage** stipitate-glandular to glandular–villous. **Leaves** cauline; blades elliptic to ovate, ovate-lanceolate, or lanceolate, (20–)30–90 mm x 5–25(–35) mm, palmately veined, margins denticulate with 1–4 pairs of teeth to subentire or entire, apex acute, base rounded or cuneate, subclasping; petioles absent. **Flowers** 2–8, axillary at leafy medial to distal nodes. **Fruiting** pedicels 45–90 mm. **Calyx** cylindric-campanulate, 15–22 mm, not inflated, stipitate-glandular to glandular–villous, lobes subequal to distinctly unequal, 5–7 mm, ovate with a linear-caudate apex, erect, not ciliate. **Corollas** light pink with darker pink stripes down the middle of each lobe, lower 3 lobes with a white basal patch, tube-throats infundibular, 20–30 mm, exserted 7–10 mm beyond calyx, strongly bilabiate, palate ridges yellow, lobe apices usually truncate and shallowly retuse, throats open. **Styles** 25–29 mm, glabrous. **Anthers** included, thecae spreading, white-villous. **Herkogamous**. **Capsule** included, narrowly cylindroid, 7–13 mm. $2n = 16$ (Vickery et al. 1958, 1963, 1986; Heisey et al. 1971).

Corolla color has been described as rose, rose-pink, pink, pink and white with yellow throat, pink with a darker stripe down center of each lobe, striped on the throat.

Flowering Jul–Aug. Springs and seeps, meadows, cliffs, steep rocky slopes, ridges; (1400–)1800–3000(–3500) m; Calif. Map 1.

Students of sect. *Erythranthe* have recognized that two morpho-geographic races exist within what has been treated as the single species *Erythranthe lewisii* (e.g., Nobs & Heisey 1965; Heisey et al. 1971; Vickery & Wullstein 1987; Beardsley et al. 2003). The Sierra Nevada race (here segregated

as *E. erubescens*), essentially restricted to Sierran California, has mostly light pink corollas. The northern race (treated here as *E. lewisii* sensu stricto), widespread from southern Alaska south to northern California, northern Utah, and northern Colorado, has mostly magenta-rose corollas (compare Figs. 3-5 with 11-13). Corolla hue in *E. lewisii* is more variable than in *E. erubescens*.

Heisey et al. (1971) noted that the Sierra Nevada race also has narrower, more lanceolate and less dentate leaves with shorter-stalked glandular trichomes. "Conceivably, the Sierran plants could merit taxonomic recognition as a subspecies, but in the present report we prefer to regard them as two regionally and cytologically differentiated races" (p. 7).

Beardsley et al. (2003, p. 1407) made parallel observations: "Differences exist in corolla color, size, shape of leaves, and in stem and branching characteristics between [*Mimulus*] *lewisii* populations in the Sierra Nevada (Sierra Nevada race) and those in the Cascade and Rocky Mountains (Northern race). ... The results of our analysis of 474 AFLP fragments indicate two very well-supported clusters (100%) that correspond to the two races. All of the *M. lewisii* from the Sierra Nevada fall into one cluster and all the *M. lewisii* from the Cascades and the Rockies fall into another, with two exceptions. *Mimulus lewisii* [Northern race NCA 08] from the Siskiyou Mountains in northern California and *M. lewisii* [Northern race WA 02] from Poe Mountain in the Cascades in Washington appear to be intermediate between the two races. **The presence of intermediates between the races and the lack of substantive evidence for reproductive isolation in nature lead us to retain *M. lewisii* as one species at the present time"** (emphasis added).

It is not clear in what sense Beardsley et al. saw a lack of evidence for reproductive isolation in nature, because the two entities are allopatric where their ranges approach each other in northern California (Map 1); prezygotic reproductive isolation presumably is complete, even though plants might rarely occur sympatrically through long-distance dispersal. Both of the samples putatively showing intermediacy (Beardsley et al. p. 1403) are within the geographic range of *Erythranthe lewisii* sensu stricto; one of them (in Washington, Chelan Co.) is deeply imbedded among typical populations of the species; existence of the other (in northern California, Siskyou Co.), whether indicating rare introgression or perhaps variation remnant from an allopatric speciation event, surely does not deflect the view that two species can be recognized. Many species across many genera are recognized even though they may form natural hybrids with others.

Postzygotic isolation also separates the northern race from the Sierran race. "When any of four northern races (Warner Mountains, [Modoc Co.] California; Stevens Pass, Washington; Mount Rainier, Washington; and Logan Pass, Montana) are crossed among themselves in any combination, all the F1 hybrids show regular pairing at meiosis and high pollen fertility. The same is true when six races of *M. lewisii* from the central Sierra Nevada are intercrossed. Pollen infertility in each of these two groups of F1 hybrids ranges from 6 to 18 percent. In contrast, F1 hybrids between any of the northern and any of the Sierran group consistently show irregularities in chromosome pairing, with two sets of quadrivalents either in chains or rings at first metaphase, and a pollen infertility of 44–67 percent" (Nobs & Heisey 1965, p. 428). Hiesey et al. (1971) interpreted this incompatibility as arising from two pairs of reciprocal translocations. Observations by Vickery and Wullstein (1987) also indicate postzygotic isolation: artificial crosses between *E. erubescens* and *E. lewisii* produced relatively high seed set but viability of seeds produced by F1s was very low (noted to constitute a "moderate crossing barrier"), perhaps reflecting the same genetic system as observed earlier by the Carnegie group.

Difference between the two subgroups of *Erythranthe lewisii* also is reflected in their genetic compatibility with *E. cardinalis*. Sierran *E. lewisii* (= *E. erubescens*) and typical *E. cardinalis* are genetically interfertile (with normal meiosis) and hybrids potentially produce advanced segregants

that may closely resemble either parent (Nobs & Heisey 1964, 1965). "In contrast, members of the northern group of [*E.*] *lewisii* when crossed with the same races of [*E.*] *cardinalis* consistently show meiotic irregularities. Two sets of quadrivalents are evident at first metaphase in the majority of the pollen mother cells, and pollen infertility is high, 60–78 per cent" (Nobs & Heisey 1965, p. 428–429).

I am not able to confirm diagnostically consistent morphological differences between *Erythranthe lewisii* and *E. erubescens* noted by Heisey et al. (1971) and Beardsley et al. (2003). But in addition to the corolla color difference, a consistent distinction is observed here in calyx morphology — in *E. lewisii* the calyx tube is measurably shorter and broader, more barrel-shaped than tubular. Correspondingly, Vickery (1990) observed that corolla throat is larger and more open in *E. lewisii* than *E. erubescens* (ca 12–15 mm wide and high vs ca. 10 mm wide by 7 mm high) — this appears to be consistent with many photos available on the internet.

Ontogenetic studies of two geographically distinct populations of *Erythranthe lewisii* and two of *E. erubescens* have revealed differences in the development of pedicels, ovaries, stamens, calyx tubes, sepals, and corollas (Hazle 2001). The ovary of *E. erubescens* is separated from the nectary by a deep invagination that does not occur in *E. lewisii* (see Hazle & Canne Hilliker 2005, Figs. 8, 9, and 10). Differences in corolla bud shape carry forward into mature corollas (*E. erubescens* with more forward-projecting lobes, *E. lewisii* with more recurved lobes) — the lower lip, including the villous palate ridges, of *E. erubescens* forms a more extended landing platform, a subtle but consistent difference (compare Figs. 4 and 5 with Figs. 11, 12, and 13). Vickery (1990) observed that the corolla lobes of *E. erubescens* are "thrust forward" while in *E. lewisii* they are "gently recurved."

In sum, typical *Erythranthe lewisii* (the northern race) and the Sierra Nevada population system are discontinuously distinct in morphology and reproductively isolated by prezygotic and postzygotic barriers. This provides a complete rationale for regarding both as distinct species.

4. ERYTHRANTHE CARDINALIS (Dougl. ex Benth.) Spach, Hist. Nat. Veg. 9: 313. 1840. *Mimulus cardinalis* Dougl. ex Benth., Scroph. Ind., 28. [17 Nov] 1835. *Diplacus cardinalis* (Dougl. ex Benth.) Groenl., Rev. Hort., sér. 4, 6: 137. 1857. **TYPE: USA. California**. "California," 1831, *D. Douglas s.n.* (holotype: K presumably; isotypes: GH digital image!, NY digital image!). Bentham's publication slightly preceded that of John Lindley (Trans. Hort. Soc. London n. ser., 2: 70, pl. 3. 1835 ["read" 4 Nov 1835; probably published in Dec 1835 or early 1836]), which also described *Mimulus cardinalis* (and illustrated it — see Fig. 14).

Specimens at BR and M (digital images!) perhaps are type material, but if so the label data are misleading (if not incorrect): each label is printed, distributed from "Herb. Soc. Hort Lond.," with "Nova California, Douglas, 1833." Douglas was in the Pacific Northwest in 1833, north of the range of *Erythranthe cardinalis*. The type was collected somewhere between Santa Barbara and San Francisco, as he explored in that area of California in 1831 (Hooker 1836; Rogers 2010); all of his California specimens presumably were shipped to England from Hawaii on 8 September 1832 (see comments under *Mimulus roseus*).

Mimulus cardinalis var. *exsul* Greene, Leaflets Bot. Observ. Crit. 2: 2. 1909. **TYPE: MEXICO. Baja California**. Cedros Island, 18-20 Mar 1889, *E. Palmer 681* (holotype: US digital image!; isotype: PH).

Mimulus cardinalis var. *griseus* Greene, Leaflets Bot. Observ. Crit. 2: 2. 1909. **TYPE: USA. California**. [Los Angeles Co.]: Santa Catalina Island, moist places, esp. stream banks, May 1896, *B. Trask s.n.* (holotype: US digital image!; isotypes: MO!, PH).

Mimulus cardinalis var. *rigens* Greene, Leaflets Bot. Observ. Crit. 2: 2. 1909. **TYPE: USA. California**. [San Bernadino Co.]: Vicinity of San Bernadino, 1000-1500 ft, 10 Jul 1896, *S.B. Parish 4189* (holotype: US digital image!; isotypes: MIN digital image!, MO 2 sheets!, NY digital image!, PH).

Perennial herbs, rhizomatous, not stoloniferous. **Stems** mostly erect to ascending, 25–75 cm, freely branched. **Herbage** sparsely to densely glandular-villous to glabrate. **Leaves**: blades elliptic-ovate to ovate or obovate, 20–90(–110) mm x 10–38(–60) mm, palmately veined, thickened, adaxially glandular-villous on veins and lamina, apex acute, base acuminate, subclasping, margins irregularly serrate to dentate; petiolar region short or absent. **Flowers** 2–12, axillary at leafy medial to distal nodes. **Fruiting pedicels** 30–90(–120) mm. **Calyx** cylindric to cylindric-campanulate, 17–28(–30) mm, not inflated, hispid-hirsute to hirsute, lobes subequal, 4–7 mm, ovate to ovate-deltate, apically attenuate-acute, not caudate, usually ciliate. **Corollas** scarlet to orange–red, rarely yellow, throat yellowish with red stripes, tube-throats infundibular, (15–)20–30 mm, exserted 2–11 mm beyond calyx margin, limbs strongly bilabiate, throats open, palate yellow–villous, red, without spots or stripes. **Styles** glabrous. **Anthers** exserted, thecae spreading, densely white-villous. **Herkogamous**. **Capsule** included, narrowly oblong, 10–16 mm. $2n = 16$ (Vickery et al. 1958, 1963, 1986; Nobs & Heisey 1965; Heisey et al. 1971).

Flowering May–Sep. Moist to wet places along streams and lakes, creek beds, canyon, arroyo, and ravine bottoms, around springs and seepage areas, floodplains, moist clearings and woods edges; (5–)50–2300(–2800) m (see Angert & Schemske 2005); Calif., Nev., Oreg.; Mexico (Baja California). Map 2.

Vickery (1992) noted that yellow-flowered populations of *Erythranthe cardinalis* occur on Cedros Island, Baja California, and in the Siskyou Mountains of Oregon. They also have been collected on Santa Cruz Island, California.

Erythranthe cardinalis has sometimes been regarded as a member of the New Mexico flora, based on the supposition (or prediction) by Martin and Hutchins (1981) that the species occurs in that state. No documenting record, however, has been encountered in the present study for *E. cardinalis* or for *E. verbenacea* or *E. cinnabarina*.

Erythranthe cardinalis is completely sympatric in overall geographic range with *E. erubescens*, partially sympatric with *E. lewisii* (Maps 1, 2), but interbreeding is rare between *E. cardinalis* and either of the other two in natural populations— in one natural sympatric population of *E. cardinalis* and *E. erubescens*, Ramsey et al. (2003) found 2 of 2336 progeny to be hybrids. Heisey et al. (1971) observed that artificial F1 hybrids between the same two are abundantly obtained, vigorous, and fertile but, apparently in contrast, Vickery and Wullstein (1987) observed low seed set in artificial F1s between *E. erubescens* (Placer Co., California) and two samples of typical *E. cardinalis* (Los Angeles and San Mateo cos., Calilfornia). Ramsey et al. (2003) found that *E. cardinalis*-*erubescens* hybrids had lower seed set, lower pollen viability (ca. one-third that of the parental species), and significantly lower seed mass than the parents, but they found little or no reduction in seed germination, survival, growth, and flowering of F1 hybrids. F2 segregants (*cardinalis*-*erubescens*) display a wide variety of form and color (Bradshaw et al. 1995). Hybrids apparently are not known between *E. cardinalis* and *E. lewisii* sensu stricto.

Compared to postzygotic barriers to gene flow, prezygotic isolation between *Erythranthe cardinalis* and *E. erubescens* is stronger (Ramsey et al. 2003). Prezygotic barriers are reflected first in their elevational segregation and then in differential pollinator visitation. Habitats of *E. cardinalis* are at (5–)50–2300(–2800) meters, while *E. erubescens* occurs at (1300–)1800–2800(–3500) meters. The two co-occur only along larger watercourses at mid-elevation sites (in the Yosemite region, the shared distribution limit is 1200–1600 meters—Angert & Schemske 2005; Angert 2006 (or 1200–1500 meters—Angert et al. 2008). As noted by Heisey et al. (1971), "seeds of [*M. erubescens*] from high elevations are occasionally carried by streams to lower sites occupied by *M. cardinalis* and establish ephemeral populations" — they studied one such site on the floor of Yosemite Valley at 1300 meters. Where the two do co-occur, their specialization to different pollinators almost

completely restricts gene flow. *Erythranthe erubescens* is bumblebee-pollinated while *M. cardinalis* is hummingbird-pollinated, the animal preferences influenced primarily by corolla color, size, and shape and nectar reward. Floral traits of these two species and their genetic basis have been the subject of numerous studies (e.g., Bradshaw et al. 1995, 1998; Schemske & Bradshaw 1999).

5. ERYTHRANTHE CINNABARINA Nesom, **sp. nov. TYPE: USA. Arizona**. Cochise Co.: Chaperon Canyon, at road, cold living brook, 7300 ft, 1 Jul 1907, *Blumer 1551* (holotype: MO!; isotypes: ARIZ!, NMC!).

Similar to typical *Erythranthe cardinalis* in its spreading anther thecae, relatively short-exserted corolla tube, and its reflexing corolla lobes but distinct in its generally larger leaves with reduced vestiture, fewer flowers, larger calyx and corolla, apically caudate calyx lobes, and its separate geographical range See details in couplet 6 of USA key above.

Perennial herbs, rhizomatous. **Stems** mostly erect to ascending, 25–60 cm, freely branched. **Leaves**: blades elliptic to oblong-elliptic, elliptic-lanceolate, or broadly lanceolate, 60–125 mm x 25–46 mm, palmately veined, thickened, adaxially glabrous to minutely (lens) stipitate- or sessile-glandular, abaxially minutely short glandular-villous along the veins, glabrous on lamina, apex acute, base narrowly auriculate, clasping to subclasping, margins shallowly dentate with sharp-pointed teeth; petiolar region absent. **Flowers** 2–4(–8), axillary at leafy distal nodes. **Fruiting pedicels** 50–95 mm. **Calyx** cylindric-campanulate, (27–)29–34 mm x 9–12 mm (pressed), not inflated, minutely stipitate- or sessile-glandular, lobes subequal, 7–10 mm, ovate, abruptly attenuate to a linear-caudate apex, usually ciliate. **Corollas** deep orange, dull orange, red-orange, deep scarlet, tube-throats tubular, 29–36 mm, exserted 7–12 mm beyond calyx margins, limbs strongly bilabiate, throats open, yellow-orange with dark red stripes leading onto the basal part of the lobes, without spots, palate ridges raised, red, densely short-villous with yellowish hairs. **Styles** glabrous. **Anthers** exserted, thecae spreading, densely white-villous. **Herkogamous**. **Capsule** included, narrowly oblong, 14–18 mm. $2n = 16$, as inferred from Nobs and Heisey (1965) and from Heisey et al. (1971).

Flowering Jun–Aug(–Sep). Canyons, ravines, stream beds and margins, riparian vegetation, mixed conifer forest; 2100–3300 m; Arizona. Maps 2, 3.

Erythranthe cinnabarina occurs in habitats at elevations of 2450–3100 meters in Cochise Co. (Chiricahua Mts.), Graham Co., (Pinaleno Mts.), and Pima Co. (Santa Catalina Mts.). *Erythranthe verbenacea*, with which it sometimes has been confused, occurs at lower elevations (350–2600 meters) and ranges over most of the state (Apache, Cochise, Coconino, Gila, Graham, La Paz, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yavapai cos.). *Erythranthe cinnabarina* apparently occurs alone (without *E. verbenacea*) in the Pinaleno Mts. and in the Chiricahua Mts., but both species have been abundantly documented in the Santa Catalina Mts., where they sometimes closely co-occur in areas of elevational overlap (e.g., at Marshall Gulch, at ca. 2500 meters; at Bear Wallow Campground, ca. 2600 meters).

Additional collections examined. **USA. Arizona**. Cochise Co., **CHIRICAHUA MTS.**: no other data, *Bloomer n-13* (ARIZ); Chiricahua Wilderness Area, Greenhouse Trail, 1/4 mi E of Cima Cabin, where trail crosses creek, 8780 ft, with *Pseudocymopteris*, *Veratrum*, *Viola*, *Fragaria*, 3 Jul 1975, *Letthlter 94* (ASU); East Turkey Creek, moist sandy soil in creek bottom, 6300 ft, 22 Jun 1960, *McCormick et al. 174* (ARIZ); Turkey Creek Canyon, 3 air mi SSW of Paradise, 7 air mi W of Portal, in the canyon W of the intersection of the road to Paradise and the Forest Service road to Onion Saddle, in soil collected between boulders present in the creek, with *Juniperus deppeana*, *Pinus chihuahuana*, *Pseudotsuga*, *Picea*, *Quercus gambelii*, *Juglans*, *Hedeoma hyssopifolium*, *Habenaria sparsiflora*, 6800–7000 ft, 9 Sep 1986, *Ward 86-034* (NMC). Graham Co: **PINALENO MTS.**: Upper Marijilda Canyon, below Shannon Camp, along creek, 9000 ft, 6 Aug 1972, *Bingham 2-18* (ASU); riparian zone at Grant Creek just below compgrounds in Mexico conifer forest, 8500 ft, 28 Jul 1988,

Bricker 331 (ASU); along AZ Hwy 366, ca. 1.5 mi NW of Hospital Flat, scattered in stream-bed under mixed conifers, 8700 ft, 7 Sep 1980, *Jenkins 3127* (ARIZ); Grant Creek, 6300 ft, 21 Jun 1983, *Johnson 1175* (ASU); Mount Graham, Jul 1927, *Kearney 4502* (ARIZ); junction of Grant Creek and Swift Trail, 10 mi E of Clark Peak Trailhead, along creek in moist mixed coniferous forest, 2665 m, 6 Aug 1990, *Lowry s.n.* (ARIZ); branch of Ash Creek, 1.1 mi NE of Columbine Work Center, along stream, 9200 ft, with *Heracleum*, *Actaea*, *Epilobium angustifolium*, 25 Jul 1989, *McLaughlin 5622* (ARIZ); Marijilda Canyon, in water and in moist soil, 8500 ft, 3 Sep 1944, *Pultz 1080* (ARIZ); Coronado Natl. Forest, adjacent to FS 803, 7.8 mi E of FS 287, S-facing slope, in gravelly alluvium, Subalpine Coniferous Forest, with *Populus tremuloides*, *Pinus flexilis*, *Pseudotsuga menziesii*, 10,000 ft, 16 Jul 1995, *Villalba 2289* (NMC). Pima County. SANTA CATALINA MTS.: 20 mi NE of Tucson, Ski Bowl winter sports area, along stream, 8 Jul 1964, *Baad 444* (VDB); Upper Sabino Creek, 1 mi W of Summerhaven, streamside, 8000 ft, 27 Jun 1960, *Barr 60-69* (ARIZ); Mount Lemmon, Jul 1965, *Hesselberg s.n.* (ARIZ); 32 mi NE of Tucson via Catalina Hwy. in Bear Wallow, mixed conifer forest, wet gulley, 8200 ft, 24 Jul 1965, *Matthews 471* (ASU, VDB); Marshall Gulch, 7600 ft, 28 Jun 1917, *Shreve s.n.* (ARIZ); Mount Lemmon, Bear Wallow Camp grounds, 8000 ft, 28 Aug 1938, *Smith 14169* (ARIZ); Upper Sabino Creek, Turkey Run Rd, 1 mi W of Summerhaven, wet stream bed, with *Mimulus guttatus* and *Platanthera limosa*, 8100 ft, 24 Jul 2008, *Tedford 814* (ARIZ); Marshall Gulch, 20 Jun 1907, *Thornber 4191* (ARIZ); Soldiers Camp, 7 Aug 1908, *Thornber s.n.* (ARIZ); Upper Sabino Canyon, in ravine, along small flowing stream, SE & NW 20 d slope, gneiss with quartzite, Stand #17, riparian mixed conifer forest, with *Abies concolor*, *Pseudotsuga menziesii*, 8500 ft, 10 Jul 1962, *Whittaker & Niering s.n.* (ARIZ).

Evidence for recognizing *Erythranthe cinnabarina* at specific rank, distinct from *E. cardinalis*, is unequivocal and compelling. In fact, very rarely has such a complete array of evidence been available for the description of a new species. The Arizona system is geographically long-disjunct from the typical *E. cardinalis* (Map 2), adapted to a different ecology, and documented to be genetically distinct, phylogenetically distinct, and distinct in morphology. Even without knowledge of their genetics, if plants of 'cinnabarina' morphology occurred in California, where they would have been subject to general comparative study, the discontinuity surely would have been recognized earlier.

Molecular studies show the two entities to have a evolutionary sister relationship. In the molecular analysis of sect. *Erythranthe* (Beardsley et al. 2003), the disjunct Arizona populations identified as *Erythranthe cardinalis* (cited as *PB 2001-01* WTU and *PB 2001-02* WTU, but vouchers not at WTU; both collected from the same population in Marijilda Canyon of the Pinaleno Mts., Arizona, fide Paul Beardsley, pers. comm.) cluster as sister to those from Oregon, California, and Mexico (*Vickery 11315*, UT) — based on AFLPs analyzed by neighbor-joining and parsimony.

Nobs and Heisey (1965) found that at least one reciprocal translocation in *Erythranthe cinnabarina* distinguishes it from populations of typical *E. cardinalis*. "A race of *Mimulus cardinalis* from the Santa Catalina Mountains [Marshall Gulch] of Arizona when crossed with any of several *M. cardinalis* races from the Pacific coast or the central Sierra Nevada in California produces F1 hybrids that have one tetravalent or trivalent plus a single chromosome in about 50 percent of the pollen mother cells. Others show regular pairing of all eight chromosomes, but often one or two pairs are loosely attached. ... Pollen infertility increases to 20–35 percent in F1 hybrids with the Arizona race, compared with 3–7 percent in various hybrids between five coastal and Sierran races. Pairing at meiosis is highly regular in the Sierran group, with no evidence of any structural differences among any of the pairs of chromosomes" (p. 427). Pollen fertility in the F1s was reduced 20–30% (Nobs & Heisey 1967). Heisey et al. (1971) noted that the Arizona 'cardinalis' "is genetically differentiated by a mild sterility barrier that appears to be the result of a reciprocal translocation between two pairs of chromosomes" but pointed to an illustration (their Fig. 9, lower right) of irregular meiotic pairing in

an F1 hybrid between *E. cardinalis* from Marshall Gulch and *E. lewisii* from Logan Pass, Montana. Vickery & Wullstein (1987) found that seed viability of F1 hybrids between typical *E. cardinalis* and *E. cinnabarina* [from Pima Co., Arizona] was very low, constituting a "strong crossing barrier."

The genetic distinction between *Erythranthe cinnabarina* and *E. cardinalis* also can be seen in their genetic relationship to *E. erubescens* and *E. lewisii*. *Erythranthe cinnabarina* is postzygotically isolated from both *E. erubescens* and *E. lewisii* — "The Arizona races of *M. cardinalis* show a high degree of genetic incompatibility with either the northern or Sierran races of *M. lewisii*. The F1 hybrids in both instances are about 87 percent sterile, and in some cultures they are sublethal" (Nobs & Heisey 1965, p. 429). In contrast, typical *E. cardinalis* is interfertile with *E. erubescens* (see comments above).

Vickery and Wullstein (1987, p. 340), following Heisey et al. (1971, 7), referred to *Erythranthe cinnabarina* as the "narrow-leafed race" of *E. cardinalis* and separated it in their key from typical *E. cardinalis* by a narrower leaf outline — but this is essentially the reverse of what is observed here, based on nearly all specimens available for examination. Nor do the measurements of calyx and corolla size by Vickery and Wullstein show the marked differences between the two species recorded in the present study.

Despite continuing confusion of *Erythranthe verbenacea* and the *E. cardinalis*-like plants (*E. cinnabarina*) in Arizona (see comments below), their distinction also is clear, with *E. cinnabarina* having different corolla morphology, different anther thecae orientation, larger, broader leaves with reduced vestiture, and different ecology. I have not seen any collection that might be indicative of hybridization, perhaps because of the demonstrated genetic incompatibility between the two. "The most highly developed genetic barrier in the *Erythranthe* section appears between the intercompatible [*E. verbenacea*, *E. eastwoodiae*, and *E. nelsonii*] ... and *M. cardinalis*. The Arizona and California forms of *M. cardinalis* are about equally incompatible with the *M. verbenaceous-eastwoodiae-nelsonii* complex" (Nobs & Heisey 1965, p. 428).

Contrasts between the two species are outlined in the couplet below.

1. Corolla tube-throat exserted 7–12 mm, exserted 3–10 mm beyond calyx margin, anther thecae reflexing; leaves 60–120 x 25–46 mm, adaxially glabrous to minutely (lens) stipitate- or sessile-glandular, abaxially minutely short glandular-villous along the veins, glabrous on lamina, habitats at 2450–3100 meters ..... **Erythranthe cinnabarina**
1. Corolla tube-throat exserted 13–25 mm beyond calyx margin; anther thecae straight, spreading; leaves 50–75 mm x 15–26(–30) mm, sparsely to densely glandular-villous on both surfaces, habitats at 350–2600 meters ..... **Erythranthe verbenacea**

6. **ERYTHRANTHE VERBENACEA** (Greene) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. *Mimulus verbenaceus* Greene, Leafl. Bot. Observ. Crit. 2: 2. 1909. *Mimulus cardinalis* Dougl. ex Benth. var. *verbenaceus* (Greene) Kearney & Peebles, J. Washington Acad. Sci. 29: 491. 1939. **TYPE: USA. Arizona**. [Yavapai Co.]: In crevices in the perpendicular walls of the cañon where the water drips out, Clear Creek, Camp Verde, 9 Aug 1891, *J.W. Toumey s.n.* (holotype: US digital image!). The US sheet has a handwritten annotation by Greene as "Mimulus verbenaceus, Type."

Mimulus lugens Greene, Leafl. Bot. Observ. Crit. 2: 3. 1909. **TYPE: USA. Arizona**. [Cochise Co.]: Fort Huachuca, 26 Apr-21 May 1890, *E. Palmer 441* (holotype: US digital image!). The US sheet has a handwritten annotation by Greene as "Mimulus lugens, Type."

Mimulus nelsonii A.L. Grant, Ann. Missouri Bot. Gard. 11: 144. 1925 ("1924"). *Erythranthe nelsonii* (A.L. Grant) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. **TYPE: MEXICO. Durango**. Sierra Madre, 30 mi N of Guanaceví, 8000-9000 ft, 18 Aug 1898, *E.W. Nelson 4775* (holotype: US digital image!; isotypes: K digital image!, PH digital image!).

Perennial, rhizomatous. **Stems** erect to decumbent, 20–60 cm, usually simple, weakly 4-angled. **Herbage** sparsely to densely glandular-villous. **Leaves** cauline; blades elliptic to obovate, rhombic-ovate, or broadly spatulate, 50–75 mm x 15–26(–30) mm, 3-5-palmately veined from the base, margins coarsely serrate distally or along the whole length, apex acute to obtuse, base subcordate, subclasping, petioles absent. **Flowers** 2–12, axillary at leafy medial to distal nodes. **Fruiting pedicels** 45–90(–110, rarely to 150) mm. **Calyx** campanulate 20–28 mm, weakly inflated, sparsely glandular-villosulous to stipitate-glandular, lobes subequal, 5–6 mm, ovate to ovate-triangular with a linear-triangular apex, erect. **Corollas** crimson, often tinged with yellow, tube-throats tubular, 25–35 mm, exserted 13–25 mm beyond calyx margin, strongly bilabiate, lower lip spreading, upper lip erect, lobe apices truncate, often emarginate, throats open, ventral ridges raised, dark red, densely short-villous. **Styles** glabrous. **Anthers** exserted, thecae reflexed, white-villous. **Herkogamous** (strongly to weakly). **Capsule** included, cylindric, 15–22 mm. $2n = 16$ (Vickery et al. 1958, 1963, 1986; Nobs & Heisey 1965; Heisey et al. 1971).

Flowering Jun–Sep. Stream edges and beds, floodplains, around seeps and springs, canyon bottoms, moist cliff crevices and ledges; 350–2600 m; Ariz., Utah; Mexico (Baja California, Chihuahua, Sinaloa, Sonora, Durango). Map 3.

The populations of *Erythranthe verbenacea* in Baja California are long-disjunct from the main range, occurring there on the east side of the Sierra Juarez in the vicinity of Tajo Canyon (a.k.a. Cantillas Cañon or Tantillas Cañon). Specimens examined. **MEXICO. Baja California**. Tajo (Cantillas) Canyon, 10 Sep 1952, *Harbison 44828* (SD, UC); Tajo (Cantillas) Canyon, 21 Apr 1955, *Harbison 111* (CAS-2 sheets); Tajo Cañon, E side of Sierra Juarez, 32° 16' N, 115° 55' W, wet sandy soil in shade of large boulder, 900 m, 8 Sep 1957, *Moran 6081* (CAS, SD); Sierra Juarez, between El Topo and Laguna Hanson, Rancho Rodeo del Rey, extreme NE part of the Ranch in the upper part of Tajo Canyon, 33.2208° N, 115.897° W, schist substrates, riparian, 1600 m, 21 Jun 2007, *Rebman 13597* (SD); Cantillas Canyon, desert canyon, 1 Apr 1953, *Schwenkmeyer s.n.* (SDSU fide SEINET). Typical *E. cardinalis* in Baja California occurs further west and south and is allopatric with *E. verbenacea*. See other comments following *E. cardinalis*.

Vickery (1992) noted that yellow-flowered morphs of *Erythranthe verbenacea* occur "in a population" at Vasey's Paradise in the Grand Canyon (Coconino County), 32 miles downstream from Lees Ferry.

Populations of *Erythranthe verbenacea* in the vicinity of Oak Creek Canyon in southern Coconino Co., Arizona (documented by numerous collections), have leaves with a narrow, lateral, undulating, purple stripe across the mid lamina (Fig. 19). The coloration is retained even in dried specimens. A similar pattern of leaf coloration occurs in *E. flammea* (Fig. 20).

Grant (1924) recognized *Mimulus verbenaceus* as a species distinct from *M. cardinalis*, a distinction later confirmed by Carnegie researchers (e.g., Nobs & Heisey 1965; Heisey et al. 1971) and by Vickery and Wullstein (1987), who found a strong crossing barrier between the two (see comments under *Erythranthe cinnabarina*). Kearney and Peebles (1942, 1960) and Shreve and Wiggins (1964) treated *M. verbenaceus* as a variety of *M. cardinalis*, while Holmgren (1984) and Welsh et al. (2003) have regarded it as a synonym of *M. cardinalis*. It currently is treated as a synonym of *M. cardinalis* by USDA (2014) and Kartesz (2014).

In Grant's description of *Mimulus nelsonii*, she remarked only that it "is unique in the section [*Erythranthe*] on account of its unequal calyx-teeth and its short style" (1924, p. 144). She did not provide comparative measurements of style length and I cannot find that it differs from *E. verbenacea* in that feature. The calyx lobes are indeed unequal in length and in this feature apparently stand apart

from typical *E. verbenacea* — this population in the Guanacevi area, at the very southernmost extension of the *E. verbenacea* range (Map 3) — is otherwise identical to *E. verbenacea*. It might be regarded as a peripheral variant of the latter, but it unequivocally is not the same species as occurs along Hwy 40 between Cd. Durango and Mazatlan, here recognized as *E. flammea*.

Molecular data (Beardsley et al. 2003) indicate that *Erythranthe verbenacea* is sister to *E. eastwoodiae* and phyletically distinct from *E. cardinalis*/*E. cinnabarina*, which is sister to *E. lewisii*/*E. erubescens*. In addition to distinction in shape and length of the corolla tube-throat (infundibular and shorter in *E. cardinalis*/*E. cinnabarina* vs. cylindric and longer in *E. verbenacea* — see key couplet 5; also see the couplet as part of discussion under *E. cinnabarina*), corolla lobes in *E. cardinalis* are reflexed while the adaxial corolla lobes of *E. verbenacea* are spreading. This is evident in living plants (see many photos via internet) but more difficult to see in pressed material. Another contrasting feature noted by Grant (1924), Heisey et al. (1971), and Beardsley et al. (2003) is anther thecae orientation — thecae are reflexed 45° in *E. verbenacea* and *E. eastwoodiae*, in contrast to the spreading (non-reflexed) lobes of *E. cardinalis*.

7. **ERYTHRANTHE EASTWOODIAE** (Rydb.) Nesom & Fraga, Phytoneuron 2012-39: 36. 2012. *Mimulus eastwoodiae* Rydb., Bull. Torrey Bot. Club 40: 483. 1913. **TYPE**: **USA. Utah**. [San Juan Co.:] San Juan River, near Bluffs, 1200-1500 m, 25-29 Aug 1911, *P.A. Rydberg* and *A.O. Garrett 9883* (holotype: NY digital image!; isotypes: NY digital image!, RENO digital image!, RM, US digital image!, UT!).

Perennial, stoloniferous, sometimes also rhizomatous. **Stems** scandent to pendent, 5–30(–40) cm, mostly simple. **Herbage** villous-glandular to minutely stipitate-glandular with gland-tipped hairs, often a mixture of longer and much shorter hairs. **Leaves** cauline; blades flabellate distally to obovate to oblanceolate or elliptic, (5–)13–40(–55) mm x 8–20(–25) mm, largest near midstem or distally, palmately 3-veined, thick, apex acute, base cuneate or rounded, subclasping, margins coarsely serrate on distal half; petioles absent. **Flowers** 2–8, axillary at leafy medial to distal nodes. **Fruiting pedicels** 10–30(–40) mm. **Calyx** cuneate-cylindric to cylindric, 15–23(–27) mm, not inflated or weakly so, glabrous or minutely stipitate-glandular to sparsely glandular-villosulous, lobes subequal, 4–7 mm, triangular-acuminate, ciliate. **Corollas** scarlet to orange-red or orange, caducous, tube-throats narrowly funnelform, 20–30 mm, exserted 5–15 beyond calyx, limb strongly bilabiate, throats open, palate puberulent, red, not spotted or striped. **Styles** glabrous. **Anthers** exserted, thecae reflexed, villous. **Herkogamous**. **Capsule** included, elliptic, 6–10 mm. $2n = 16$ (Vickery et al. 1963; Nobs & Heisey 1965; Heisey et al. 1971).

Flowering May–Sep(–Nov); seepage in sandstone overhangs, cave roofs, walls, crevices, and cliff bases, pinon-juniper woodland; 900–2000 m; Ariz., Colo., N.Mex., Utah. Map 3.

The range of *Erythranthe eastwoodiae* appears to be essentially contiguous with that of *E. verbenacea* in the Grand Canyon region, but among the specimens I have studied, there has been no evidence of hybridization.

8. **ERYTHRANTHE FLAMMEA** Nesom, **sp. nov**. **TYPE**: **MEXICO. Durango**. Sierra Madre Occidental, between Mazatlán and Durango, 2 mi E of El Espinazo, 20.5 mi E of El Palmito, ledges of cliff face, in spring water, 8600 ft, 8 Jun 1962, *P.C. Hutchinson 2506* (holotype: MO!; as noted on the label, duplicates distributed to E, F, G, HEID, K, M, MEXU, MICH, NY, P, S, UC, US, WIS).

Differing from *Erythranthe verbenacea* in its reduced vestiture, longer and narrower leaves, longer corolla tube-throats, and narrowly triangular calyx lobes with an elongate, linear apex.

Perennial, rhizomatous. **Stems** erect, often laxly, 15–50 cm, moderately to densely short glandular-villous. **Leaves** cauline; blades narrowly lanceolate, 30–95 mm x 7–15(–20) mm, palmately 3-veined from the base, Hwy 40 populations with a broad, lateral, often arching, maroon stripe at the distal 1/2–1/3, moderately to densely short glandular-villous, margins sharply serrate on distal 2/3–2/5 with 8–16(–25) pairs of teeth or denticles, apex acute, base narrowly subcordate, subclasping; petioles absent. **Flowers** 6–10(–12), axillary at leafy medial to distal nodes. **Fruiting pedicels** 50–90 mm. **Calyx** broadly cylindrical, 34–37 mm, tube 20–25 mm, sparsely short villous-glandular, lobes subequal, narrowly triangular with a linear apex, 7–11 mm, erect. **Corollas** crimson-red, tube-throat cylindrical, 40–45 mm, exserted 18–20 mm beyond calyx, strongly bilabiate, throat ampliate, lobes of upper lip erect, those of lower lip shorter and spreading. **Styles** glabrous. **Anthers** exserted, thecae reflexed, densely white-villous; style exserted, glabrous. **Herkogamous** (weakly, the stigma slightly or not at all beyond level of upper pair of anthers). **Capsule** included, cylindroid, 10–12 mm. $2n = 16$ (Vickery et al. 1963; Nobs & Heisey 1965; Heisey et al. 1971). Figures 20, 21.

Flowering Jan–Jul. Cliffs, steep banks and hillsides, canyon slopes, usually in seepage or near waterfalls, pine and pine-oak woods; 6500–9000 ft; Mexico (Durango, Nayarit, Sinaloa). Map 4.

Additional collections. **MEXICO**. **Durango**. Moist area along Mex Hwy 40 near crest of mts. between Durango and Mazatlan, 9000 feet, 3 Jun 1963, *Bell 17703* (ASU, SMU); 10 to 12 mi W of La Ciudad (38 to 40 mi W of El Salto), along road to Mazatlan from Cd. Durango, steep, moist canyon slope in pine-oak forest, 8300 ft, 15 Jun 1951, *Gentry 10611* with Gilly (ARIZ); 99.1 mi W of Durango City via Hwy 40 (Mazatlan-Durango hwy), next to waterfall, uncommon, 7930 ft, 11 Jan 1977, *Goldberg 77-68* with Inouye (ARIZ); Mpio. de Súchil, Arroyo El Temascal, 4 km al SW de Piedra Herrada (La Michilia), a orilla de arroyo, muy abundante, 3 May 1981, *S. Gonzalez and M. Gonzalez 1638* (ASU digital image!, MO); along Mexican Hwy 40 from Durango to Mazatlan, along mountainous roadside, with pines and some open grasslands, 6200-8595 ft, 1 Jun 1966, *Pearce 2324* (ARIZ); Mpio. El Salto, Sierra Madre Occidental, along Hwy 40 at the eastern end of El Espinazo de Diablo, 11.3 mi SW of La Ciudad, 16 mi E of Revolcaderos, humid pine-oak forest on SE-facing cliffs and steep banks, on a roadside seep, 7800 ft, uncommon preennial, flowering & fruiting, 26 Mar 1984, *Sanders 4881* (ARIZ); Mpio. El Salto, above Los Bancos, near km post 162 on Hwy 40 (Durango-Mazatlan), dry and rather brushy S-facing slopes near the rim of the plateau, but also with localized seeps and springs, pine-oak forest with *Ceanothus*, *Cercocarpus*, *Almus*, and *Arbutus*, area heavily grazed, 8036-8397 ft, 14 Apr 1999, *Sanders 22648* (UCR); ca. 11.5 mi W of La Ciudad along Mex 40, on and around a spring flowing of a rock cut, 30 Mar 1974, *Taylor & Taylor 15830-B* (BRIT); Mex Hwy 40, near KM 161, among large granite boulders, by mountain stream in pine-oak forest, 7850 ft, 12 May 1976, *Vickery cult. no. 12,217* (MO); 50 km S of Cd. Durango on road to La Flor, 6800 ft, 10 May 1981, *Walker 81-24* (ARIZ). **Nayarit**. Mpio. El. Nayar, 100 airline km NNE of Tepic, rocky ridge with *Pinus*, *Quercus*, and *Arbutus* dissected by a grassy, spring-filled valley along the Arroyo Santa Rosa W of Santa Teresa, 2095 m, 21-24 Oct 1979, *Breedlove 44516* (MO). **Sinaloa**. On the Durango-Villa Union hwy at Km. 1164, ca. 1 mi NW of El Palmito, a small stream drains the area, flowing into the drainage of the Rio Balahurte, massive cliffs present, pine-oak forest, 6500 ft, 27 Apr 1966, *Hubbell s.n.* (ARIZ).

These plants (including all those in published chromosome, genetic, and phylogenetic studies) have previously been identified as *Mimulus nelsonii*, but the type of *M. nelsonii* clearly belongs with the earlier-described *M. verbenaceus* and is now placed there as a synonym. When Grant (1924) described *M. nelsonii*, she knew it only from the type from north-central Durango — she did not see any collections from the area to the south where all collections of *Erythranthe flammea* have been made.

Plants from southeast of Cd. Durango and in northern Nayarit should be studied more closely in comparison to those between Cd. Durango and Mazatlan, as the collections cited here (*Gonzalez &*

Gonzalez 1638, *Walker 81-24; Breedlove 44516*) tend to have broader, more densely toothed leaves (10–16(–25) pairs of teeth or denticles along the distal 2/3 vs. 8–12 pairs along the distal 2/5) without a purple cross-stripe. The calyx lobes, however, have linear apices and the corolla tube-throat is elongate (ca. 40 mm), and the close geography of all these populations suggests that they are most closely related among themselves.

9. **ERYTHRANTHE RUPESTRIS** (Greene) Nesom & Fraga, Phytoneuron 2012-39: 37. 2012. *Mimulus rupestris* Greene, Leafl. Bot. Obs. Crit. 2: 3. 1909. **TYPE: MEXICO. Morelos**. Sierra de Tepoxtlan, wet cliffs, 7500 ft, 6 May 1900, *C.G. Pringle 8348* (holotype: US digital image!; isotypes: K digital image!, MO!, NDG digital image!, PH digital image!, POM, S digital image!).

Perennial, rhizomatous. **Stems** mostly prostrate to ascending, often laxly, 5–15 cm, frequently rooting at the nodes, densely and finely glandular-villous. **Leaves** cauline; blades oblanceolate to elliptic-oblanceolate, 20–45 mm x 6–20 mm, palmately 3-veined from the base, green on both sides, moderately to densely short glandular-villous, margins shallowly to coarsely serrate on distal 1/2 with 3–5 pairs of teeth, apex acute, base gradually attenuate, slightly subclasping or not at all; petioles absent. **Flowers** 2–6 at distal nodes. **Fruiting pedicels** 20–30 mm. **Calyx** cylindric, 17–20 mm, tube 14–16 mm, moderately short glandular-villous, not ciliate, lobes subequal, triangular to ovate-triangular with a slightly attenuate apex, 3–5 mm, erect. **Corollas** crimson-red, tube-throat cylindric, 25–30 mm, exserted 13–15 mm beyond calyx, strongly bilabiate, throat ampliate, lobes of upper lip longer, erect, those of lower lip shorter and spreading. **Styles** glabrous. **Anthers** exserted, thecae reflexed, densely white-villous; style exserted, glabrous. **Herkogamous** (weakly, the stigma barely above level of upper pair of anthers). **Capsule** included, ellipsoid, 6–8 mm. $2n = 16$ (as inferred from Vickery et al. 1986).

Flowering Apr–May. Wet cliffs; 5900–7500 ft; Mexico (known only from the type and collections from near the type locality in north-central Morelos). Map 4.

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Figure 2. *Erythranthe lewisii*. Plate 20 (the lectotype) from Pursh's *Flora Americae Septentrionalis*, 1814. The corolla was described as "beautiful pale purple" with dark lines

Figure 3. *Erythranthe lewisii*. Pierce Co., Washington, Mt. Rainier National Park. Photo © Walter Siegmund, 25 August 2010. From Wikipedia

Figure 4. *Erythranthe lewisii*. Baker Co., Oregon, Elkhorn Mountains. Photo © Christopher L. Christie, 21 August 2004.

Figure 5 *Erythranthe lewisii* Beartooth Mountains in Park County, Montana Photos by Steve Torna, August 2013, used by permission from his Knowledge and Light website

Figure 6 *Mimulus roseus* From protologue in Edwards's Botanical Register by John Lindley (1833) Corolla color described as "rosea" Illustration by Sarah Ann Drake

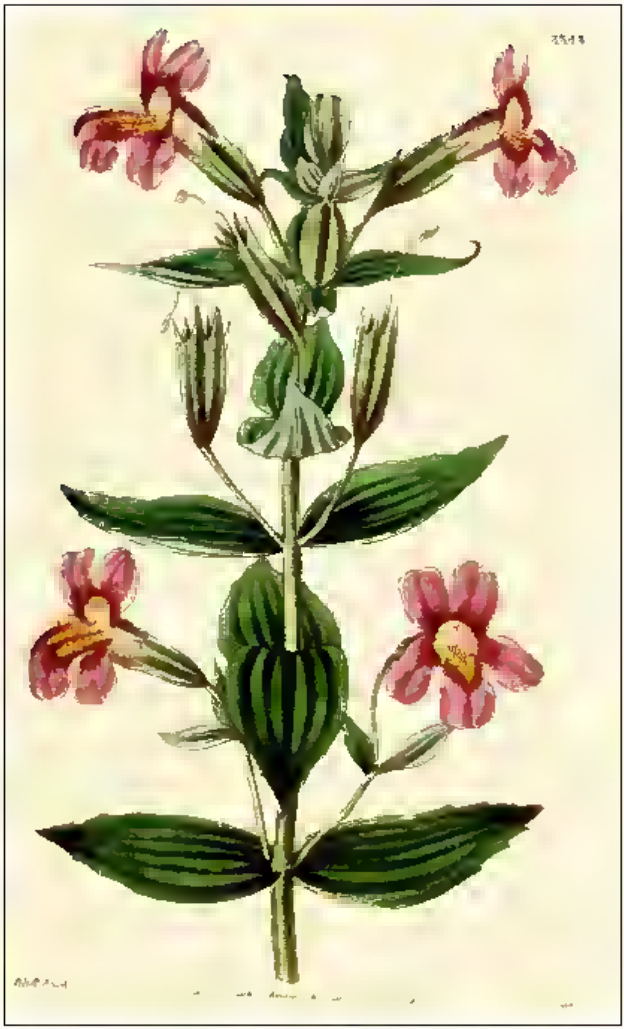

Figure 7 *Mimulus roseus* From entry in Curtis's Botanical Magazine by William Jackson Hooker (1834) Corolla described as of a beautiful rose colour Illustration by Walter Fitch

Figure 8 *Mimulus roseus* From entry in Loddiges Botanical Cabinet by George Loddiges (1835) No description was provided apart from the illustration by George Cooke

Figure 9 *Mimulus roseus* From entry in The British Flower Garden by David Don (1835) Corolla described as of a deep rose-colour We are indebted to Mr Knight, of the Exotic Nursery King's Road, Chelsea, for the specimen whence our drawing was taken. Illustration by J T Hart

Figure 10 *Mimulus roseus* Herbarium M, distributed by the Herb Hort Soc London but probably not type material Rather the plant probably was grown in London from seed either from the original California seed collection of 1831 by D Douglas or from descendants of the original cultivars

Figure 11. *Erythranthe erubescens*. Top left, Fresno Co., California, photo by Brother Alfred Brousseau, 1 Aug 1986. © 1995 Saint Mary's College of California. Top right, Madera Co., California, photo © Jeffrey Pippen, 10 Jul 2007. Bottom, Mariposa Co., California, photo © John Game, 1 Jul 2000.

Figure 12. *Erythranthe erubescens*. Alpine County, California, Ebbetts Pass. Photo by J.T. Vale, 1 Aug 1974. Cal Academy slide #T 107 885.

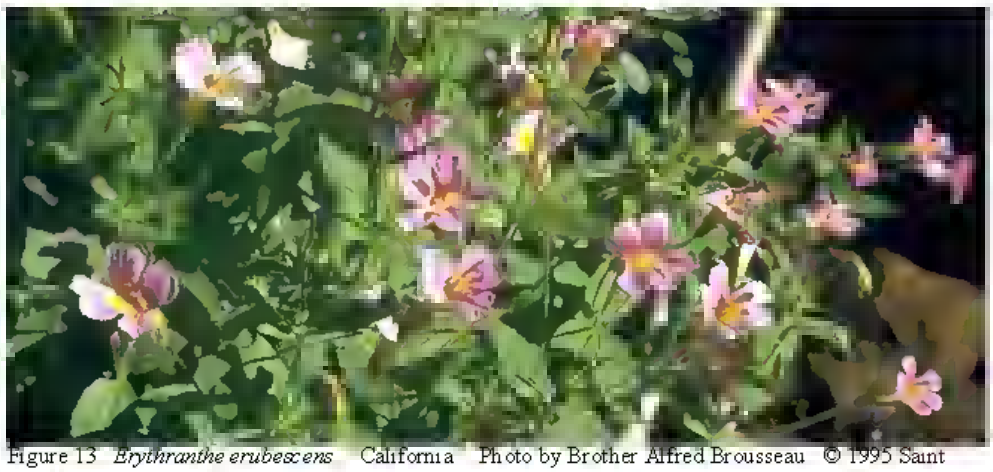

Figure 13. *Erythranthe erubescens*. California. Photo by Brother Alfred Brousseau. © 1995 Saint Mary's College of California.

Figure 14. *Mimulus cardinalis*. From entry in the Transactions of the Horticultural Society of London by John Lindley (1835). Illustration by Sarah Anne Drake

Figure 15. *Erythranthe cardinalis*. In the flood channel of Seiad Creek, near Seiad Valley, Siskyou Co., California. © 2011 Aaron Schusteff, photo 3 July 2007.

Figure 16. *Erythranthe cinnabarina*, Pinaleno Mts., Graham Co., Arizona, 24 June 2012. Photo by Bob Beatson, Flickr, used by permission. Note the large leaves, large flowers, and few-flowered inflorescences.

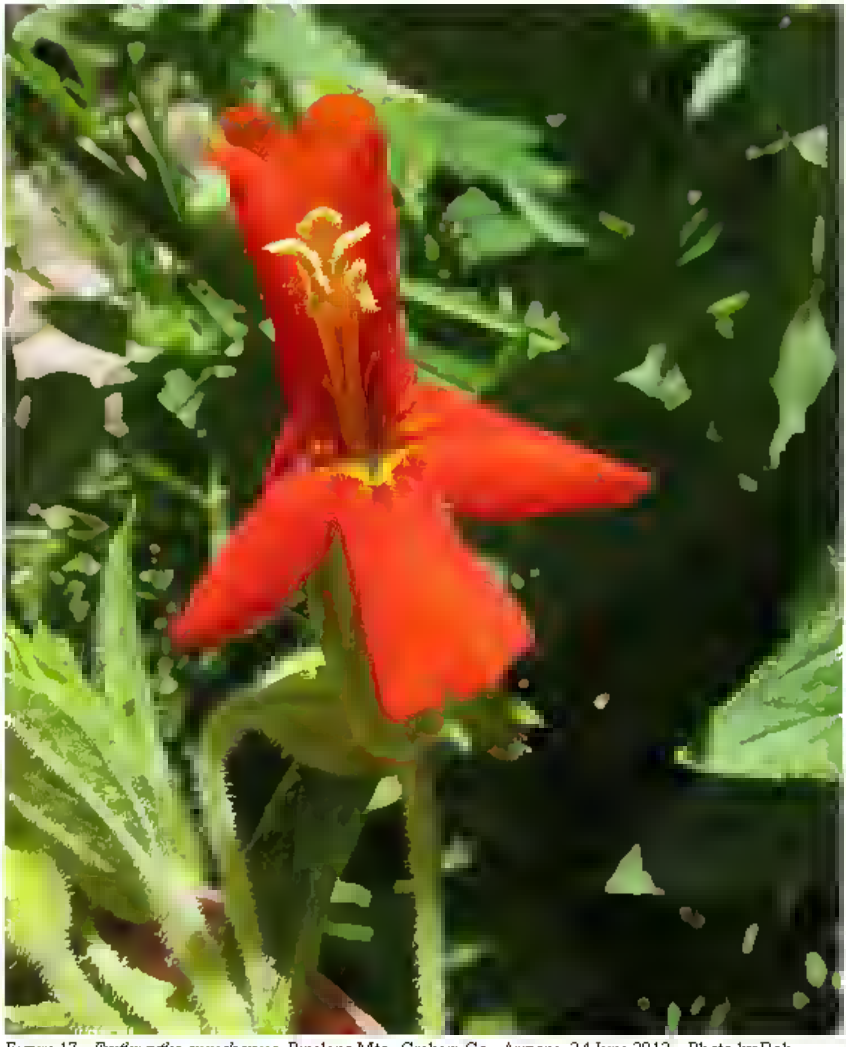

Figure 17 *Erythranthe cinnabarina*, Pinaleno Mts., Graham Co., Arizona, 24 June 2012. Photo by Bob Beatson, Flickr, used by permission. Note apparent 'infolding' of margins of upper petal pair, which seems to be the reverse of the direction of folding in *E. cardinalis*. The apparent yellow hairy palate ridges also are not characteristic of *E. cardinalis*.

Figure 18 *Mimulus verbenaceus* Painting by Mary Vaux Walcott (1925) As noted by Rogers (2010) this plant was from along the Bright Angel Trail in the Grand Canyon Coconino Co Arizona It was identified by Walcott as *M. cardinalis* but instead clearly is *M. verbenaceus*

Figure 19. *Erythranthe verbenacea*. Mazatzal Mts., Pima Co., Arizona. Photo by M. J. Plagens, 17 May 2008. From Wikipedia.

Figure 20. *Erythranthe verbenacea*. Oak Creek Canyon, Coconino Co., Arizona, 23 May 2009. The purple stripe across the leaf lamina apparently is consistenstly characteristic of plants of the Oak Creek Canyon area. Photo by Thomas H. Kent at FloraFinder.com.

Figure 21. *Erythranthe flammea*. Along Hwy 40, W of La Rumarosa, Durango, Mexico. Photo by Mark Egger, 14 Apr 1999. The purple stripe across the leaf lamina is characteristic of the species in the Cordilleran populations but not elsewhere.

Figure 21. *Erythranthe flammea*. Durango, Mexico, same population as above. Photo by Mark Egger, 14 Apr 1999.

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FOUR WATER-SOLUBLE MOUNTING MEDIA FOR MICROSLIDES

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ABSTRACT

Four mounting media for plant samples, particularly bryophytes, on microslides were surveyed: PVOH-glycerin, glycerin jelly, water-glass-glycerin, and pure glycerin with stabilized cover slips. Each was found valuable for particular uses. The new polyvinyl alcohol and glycerin mountant ("glycerine-glue") proved better than the others for general work. Details of formulae and technique are given.

There have been many publications recommending various water-soluble mounting media for making temporary or semi-permanent slide preparations for microscopic examination (e.g. Anderson 1954; Bowers 1964; Creaser & Clench 1923; Davis 1909; Frahm 1990; Lightowlers 1981; Sayre 1941, Zander 1983, 1997). Discussions by various bryologists on the bryological listserver Bryonet have been productive in describing details of methods of effectuating such mounts, with greater or lesser success.

Recent work in my lab has settled on four different mounting media, all based on glycerin (glycerol). Only glycerin has the several excellent qualities of being rather stable over time (low evaporation rate, high boiling point), being miscible with water, has least osmotic effect on cells, high index of refraction, speed of preparation, inexpensive, and, lastly but not least, being non-poisonous. Each of the four methods involves dealing with the fact that glycerin is a thick liquid and can slowly run off a slide that is tilted. Although keeping glycerin mounts in a sealed cabinet with a dish of glycerin to saturate the air may retard evaporation, glycerin will eventually evaporate and air will penetrate under the cover slip. All attempts to quickly seal (lute) a preparation so the glycerin *never* evaporates are here considered futile, as any glycerin or finger oil on the slide, or differential expansion of the glass and mountant, damages the seal. Glycerin can be attacked by microorganisms, so one can optionally add a crystal of thymol to avoid bacteria and fungi. Note that glycerin dissolves (eventually) calcium carbonate.

Much of the problem with glycerin-based and other mounting media, such as Hoyer's Solution (Anderson, 1954) or polyvinyl lactophenol (Frahm, 1990), is that osmotic effects may collapse the cells of the mounted specimen of sensitive, thin-walled species. Efforts to slowly infiltrate the specimen with glycerin, such as a drop on the margin of a water mount, are tedious and often unsatisfactory. The secret is to allow initial collapse when glycerin is applied to water-soaked material, but to then heat the slide at low temperature on a hot plate or coffee warmer. The cells of the material mounted in the water and glycerin mixture plump up quickly and stay that way as the water evaporates on the hot plate or later over time. If clearing is desired, first dip the moist plant in lactic acid for a minute or so (or heat in lactic acid) before preparing the mount. Do not stack slides for long as the pressure will squeeze glycerin from the mounts.

PVOH-GLYCERIN OR "GLYCERIN GLUE"

This is simply a 1 to 1 mixture of glycerin and a thick, syrupy solution of polyvinyl alcohol in water, or more conveniently, a ready-made polyvinyl alcohol-based glue, such as Elmer's Washable

Clear School Glue™ or Colorations™ Washable Clear Glue, both available on the Web. Add a small quantity of water to the pure glycerin first and stir in well to enhance later mixing with the glue. Heat will help disperse the glue in the slightly aqueated glycerin. The Elmer's and Colorations clear glues are apparently mostly or all polyvinyl alcohol in water. A test found that pure polyvinyl alcohol (polyvinyl alcohol 98.1–98.8%, Carolina Biological Supply) in powder form dissolved in water (about 20%, see Woods, 1997) to make a thick syrup acts much the same, but remained somewhat cloudy. Perhaps the commercial glues have a better mixing protocol. Premixed polyvinyl alcohol in water from Carolina Biological Supply worked as did the glues, demonstrating that PVOH was indeed the effective ingredient in the clear glues, but the four percent solution was too weak to set the glycerin well.

The index of refraction of PVOH-Glycerin remains high. When water in the glue evaporates in a day or two it makes a firm mount that is solid enough for mailing. If the cells of the mounted specimen collapse, heat on a hot plate or cup warmer, but collapse is rare.

Both glycerin and polyvinyl alcohol are slightly hygroscopic, but that seems to contribute no adverse effects. If PVOH powder is used rather than prepared glue, heat the powder in water vigorously for a long period to make sure the granules dissolve. Do not try to dissolve powdered PVOH in glycerin or glycerin-water as the solution becomes opaque.

Positive: No heating is necessary to melt the mountant. There are no restrictions on stains (its pH is neutral), and plants retain diagnostic colors with 2% KOH wetting solution. One can manipulate the specimen directly in the medium. The formula is simple and ingredients easily obtained. Old slides are easily soaked to remove the cover slips and refurbish. *Negative:* The exact ingredients in the clear glues are proprietary. Three or four drops of PVOH-Glycerine are necessary on a slide because the medium evaporates about 1/4 to 1/2 of its bulk in water. This is the best mounting medium I have ever used in more than 50 years of bryological study.

GLYCERIN JELLY

Take 1 packet (7 g) of Knox gelatin. Mix and let stand for a while in 50 ml cold water to hydrate. Heat but do not boil while still stirring, until the liquid is clear or at least there is no undissolved gelatin. Add glycerin to 300 ml. Heat gently for about an hour until the liquid is clear. Too much gelatin makes the jelly difficult to melt and included bubbles found on the slide will not burst.

Pour on a clean pan or plate with a flat bottom to make a thin layer. PVC (polyvinyl chloride) pans work well but any plastic that does not adhere to gelatin is acceptable. Leave uncovered (drape a cloth if air is dusty) overnight or a couple of days to allow most of the water to evaporate. Peel off the thin, flat sheet of glycerin jelly. Roll the sheet into a long tube. Slice the roll crosswise into neat, tight curlicues or helixes about 1/4 inch wide. Keep in a plastic box. Pinch off a small piece when wanted. The flat sheet of glycerin jelly will be hard to remove from the pan unless the water portion has evaporated. It is best to evaporate the water portion with heat since glycerin absorbs water, to some extent, from the air. If there are bubbles, reheat in a beaker (a water bath is helpful) and let stand as liquid.

Put plant material on a slide in water, or KOH solution (Zander 1993) or Acrosol solution (Zander 1997), soak well to eliminate air in cells. Take a strip of glycerin jelly and pinch off a small portion, put on the slide with the material, and heat on a hot plate or cup warmer (the kind that plugs in the wall is best). Try not to boil as bubbles are difficult to eliminate. Arrange material and gently add a cover slip. Although you can put a dropper bottle of glycerin jelly on a hot plate to keep it

liquid, the heat eventually turns the jelly brown, and the gelatin breaks down so that it will not harden. Some of the above is presented by Zander (1997).

Positive: Mounted plant material does not move at all; there is no sloshing or gradual settling to one side. The mount hardens in a minute and may be mailed when cool, almost immediately after labeling. Little water is present so no pockets develop from evaporation. *Negative:* Bubbles, if they form, seldom disappear. Heating must be carefully done. Operations on the material, e.g., sectioning, cannot be done in cool, solidified glycerin jelly.

WATER-GLASS-GLYCERIN

A water glass and glycerin mountant (WGG) was investigated. This seems to work well, but is not suitable for immediate mailing or other disturbance as it must dry for a day or so. The formula is simply 2 parts water-glass (sodium silicate solution 40–42 Baumé, Carolina Biological Supply), and 1 part glycerin that is previously mixed with a little water to help it dissolve in the water-glass.

Mix and stir well. Put in capped squeeze bottle or dropper bottle, but not a glass-stoppered bottle (the sodium silicate seals the plug). Several drops on a slide are necessary because much water will evaporate. The WGG solution will dry fastest around the cover slip edges and hold the slip on tightly in a day or two. The high index of refraction and tinting of leaf cells by the highly basic water-glass may allow easy anatomical analysis of *Sphagnum* species without staining. If a stain is needed, however, only basic stains are useful in this particular mounting medium. Safranin O, for instance, works fine, but toluidine blue, orcein, and methyl green precipitate out.

If the specimens have collapsed leaf cells after mounting, put the slide on a hot plate until the liquid under the cover slip just boils. Over a month or two of time, a whitish or brownish deposit may accumulate just within the margins of the cover slip, as water glass migrates to the edges and precipitates. This leaves a perfectly clear large central portion of the cover slip that is mainly glycerin held fast by the peripheral water-glass.

Creaser and Clench's (1923) paper advises far more water-glass (12:1 water glass to water) than is suggested above, but the medium is then too harsh osmotically. The present 2:1 method uses water-glass to hold the glycerin to the microscope slide, while Creaser and Clench's 12:1 method uses glycerin to keep the water-glass from crystallizing. Those who find that the WGG formula of 2:1 results in slides that are too syrupy might use 3:1.

Positive: No heating is necessary. The solution is basic and moss plants may show interesting, strong, characteristic and permanent color reactions similar to those obtained with KOH solution. *Negative:* The water-glass crystallizes out around the cover slip margins and looks messy. The large amount of water in the water-glass solution allows air pockets to form under the cover slip in thick mounts as it evaporates, and additional solution must be added. One is limited to basic stains.

PURE GLYCERIN WITH COVER SLIP STABILIZER

Soak plant in water or 2% KOH solution. Add 3-4 or more drops of glycerin. Heat to drive off most or all of the water over a coffee warmer. Put a clear PVOH glue as noted above around the cover slip margins using a small brush or applicator. The clear glue is used to hold the cover slip in place, not to prevent the glycerin from evaporating.

Because the glycerin mountant and PVOH stabilizer are both soluble in water, when the glycerin does begin to dry up, the slide is easily soaked or steamed to remove the cover slip, and the specimen remounted. One can, in fact, dunk the whole slide or that portion with the cover slip into diluted (half water and half glue) commercial clear glue, and let it dry on a slanted wire rack. The

glue covers the cover slip in a thin, flat, optically transparent film, and does not restrict casual examination.

Positive: The index of refraction is very high and cell details are superb. Few or no bubbles are evident after heating, while glycerin jelly often seems to retain any bubbles from heating. The mounts do not shrink because any water is already evaporated on heating. *Negative:* Do not leave anything heavy on the slide since it is easily disturbed. A tilted slide may allow fragments under the cover slip to migrate.

SUMMARY

Different methods are best for different applications. Glycerin jelly is best for making mounts for illustration as the plant parts do not migrate, and it is a proven long-term though not permanent mountant. Water-glass-glycerin is acceptable when color reactions of species to alkalis are studied. PVOH-glycerin is best for all-around quick mounts and is here recommended for general use. Pure glycerin has the highest index of refraction and thus provides the best viewing and may be optimal for critical or irreplaceable material, because old material, when glycerin is mostly evaporated, is easily retrieved with hot water or steam.

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VALIDATION OF THE NAME *LECHEA TORREYI* VAR. *CONGESTA* (CISTACEAE)

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ABSTRACT

Although widely used for plants of the southeastern United States, the name *Lechea torreyi* var. *congesta* was never validly published. The oversight is corrected here, and the differences between *L. torreyi* var. *congesta* and the nominate variety are discussed.

The genus *Lechea* Kalm. ex L. comprises 18 species of perennial herbs and subshrubs widely distributed across eastern North America southwestward to Texas, New Mexico, and Mexico, with representatives in the West Indies (Cuba) and Belize. While members of the genus are distinct and easily recognized, accurate species determinations often prove difficult. Species are often delimited on the basis of minute or technical characters such as capsule width and seed length or the relative lengths of the inner and outer sepals. Plants collected early in the growing season, before fruits are fully mature, may prove impossible to identify with certainty. When available, regional taxonomic treatments, such as those of Barringer (2004) and Spaulding (2013) can prove to be invaluable resources for making determinations.

At present, the only comprehensive taxonomic treatment of the genus is that of Hodgdon (1938). In this treatment, Hodgdon recognized one new species (*Lechea mensalis*) and eleven new varieties:

L. villosa Ell. var. *macrotheca* and var. *schaffneri* (both now included in *L. mucronata* Raf.);
L. tenuifolia Michx. var. *occidentalis*;
L. intermedia Leggett ex Britt. var. *depauperata*, var. *juniperina*, and var. *laurentiana*;
L. maritima Leggett var. *subcylindrica* and var. *virginica*;
L. leggettii Britt. & Hollick var. *monilliformis* and var. *ramosissima* (both now treated as varieties of *L. pulchella* Raf.); and
L. torreyi Leggett ex Britt. var. *congesta*.

The latter name, however, was not accompanied by a Latin diagnosis and is therefore invalid; this oversight is corrected here.

Lechea torreyi Leggett ex Britton var. **congesta** Hodgdon ex Lemke, **var. nov.** **Type. UNITED STATES. Florida.** Duval Co.: Dry pine-barrens, ne Florida, Aug, *A.H. Curtiss 232** (holotype: NY; isotype: NY).

Similar to *Lechea torreyi* Leggett var. *torreyi* in the brownish-green coloration of the plant, the densely-appressed pilosity of the stems, the small size of the capsules (<2 mm diam.) and the coastal plain distribution, but differing in its compact, ascending branches, markedly rust-colored inner sepals, crowded or clustered fruits, and the presence of three seeds per capsule.

Plants perennial herbs; **aerial stems** 20–40 cm tall, dull brownish-green, densely appressed-pilose; **basal stems** lacking; **leaves** with petioles not well-differentiated from the blades, the blades linear to narrowly elliptic, 10–20 mm long, 1–1.5 mm wide, with adaxial surface glabrous and abaxial surface pilose; **inflorescence** a compact panicle, the branches crowded and strongly ascending to

suberect; **flowers** crowded or fascicled on short side branches, the inner sepals longer than the outer sepals, at maturity the calyx strongly rust-colored giving a reddish cast to the plant in fruit; **capsules** ovoid, 1.5–1.7 mm long; **seeds** 3, slightly dorsiventrally compressed.

Leggett (1878) was the first author to note that there are two recognizable elements within the populations now assigned to *L. torreyi*: plants with calyces dark brown to slightly rust-colored and densely pilose with cinereous pubescence, the capsules loosely arranged or scattered and containing 4 to 6 seeds — and plants with calyces markedly rust-colored and pubescence not conspicuously cinereous, the capsules densely clustered and containing 3 seeds. Hodgdon was the first to accord formal recognition to these entities, applying the name *L. torreyi* var. *congesta* to plants with densely congested inflorescences and 3-seeded capsules, although as noted above this name was not validly published. With a distribution spanning South Carolina, Georgia, Florida, Alabama, Mississippi, and a disjunct occurrence in Belize, var. *congesta* is the more common and widespread variety of the species (var. *torreyi* is restricted to Florida).

In their treatment of *Lechea* in the southeastern USA, Wilbur and Daoud (1961) chose to not recognize varieties within *L. torreyi*. Although they accepted the distinction between 3-seeded and 4- to 6-seeded plants, these authors felt that the other morphological differences were "certainly not striking or clear-cut and . . . rather subjective in nature." More recent authors, however (e.g., Weakley 2012 and Spaulding 2013), have followed Hodgdon in recognizing the two entities. While acknowledging that additional fieldwork is needed to ascertain whether true geographic or ecological separation exists between the varieties, the forthcoming treatment of *Lechea* for the Flora of North America (Lemke, in prep) will maintain Hodgdon's segregation of *L. torreyi* into two varieties.

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BARCODING THE ASTERACEAE OF TENNESSEE, TRIBE SENECIONEAE

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ABSTRACT

Results from barcoding studies of tribe Senecioneae for the Tennessee flora using data from the nuclear ribosomal ITS marker region are presented and include first complete reports of this marker for 3 of the 15 species of these tribes that occur in the state. Sequence data from the ITS region separated all Tennessee species of *Arnoglossum*, *Erechtites*, *Hasteola*, and *Rugelia* (all of which are native) from one another and from other, non-Tennessee congeners. In contrast, many of the species of *Packera*, both from the state and from other parts of the southeastern USA, had basically identical ITS sequences. The contrast in the distinctiveness of *Arnoglossum* species compared to those of *Packera* suggests the two genera have had different histories of introduction and diversification in southeastern North America.

Tribe Senecioneae is one of the largest in Asteraceae and with a worldwide distribution has had the opportunity to diversify in many different regions. The boundaries and circumscription of the tribe have, however, changed over the past few decades, and its generic level circumscription is still being settled (Nordenstam et al. 2009; Pelser et al. 2007, 2010). Notable is the problem of the circumscription of the huge *Senecio* (ca. 1000 species), but changes have also affected other genera from the southeastern USA, most notably the recognition of *Arnoglossum* and *Hasteola* as distinct from *Cacalia* (Anderson 1974). The nuclear ribosomal ITS region has been surveyed widely in studies of the tribe (Bain & Golden 2000; Pelser et al. 2007, 2010), but there has never been a focus on species that occur in the southeastern USA, and some species remain unsampled. The current study continues the effort to survey the molecular diversity found in species of Asteraceae in Tennessee (Schilling & Floden 2012, 2013; Schilling 2013), with an increasing emphasis on revealing patterns in levels of interspecific differentiation in the ITS marker, in addition to its potential use as a barcoding region.

Senecioneae is represented in Tennessee by 7 genera and 15 species (Chester et al. 2009), of which all but two species are considered to be native members of the flora. The non-natives are *Senecio vulgaris* and *Tussilago farfara*, both widespread elsewhere as weeds and considered potential threats as invasives. Other species formerly recognized within *Senecio* in Tennessee are now placed in *Packera* (Löve & Löve 1976; Bain & Golden 2000). Several species of the tribe are listed as rare in Tennessee (Crabtree 2012), including *Arnoglossum plantagineum*, *Hasteola suaveolens*, *Packera schweinitziana*, and *Rugelia nudicaulis*, but of these only the monotypic *Rugelia* is rare globally. Also listed as rare in Tennessee is *Packera plattensis*, although it has been proposed that Tennessee populations previously assigned to this species be recognized as *P. paupercula* var. *appalachiana* (Mahoney & Kral 2008).

The goal of this study was to complete the sampling for the ITS marker for all species of Senecioneae that occur in Tennessee. Particular emphasis was placed on the two genera *Arnoglossum* and *Packera*, which exhibit radiations in southeastern North America, and sampling of additional species of both genera from areas of southeastern North America outside of Tennessee was done to allow evaluation of the overall patterns of diversification and to compare them to other Asteraceae genera of the region.

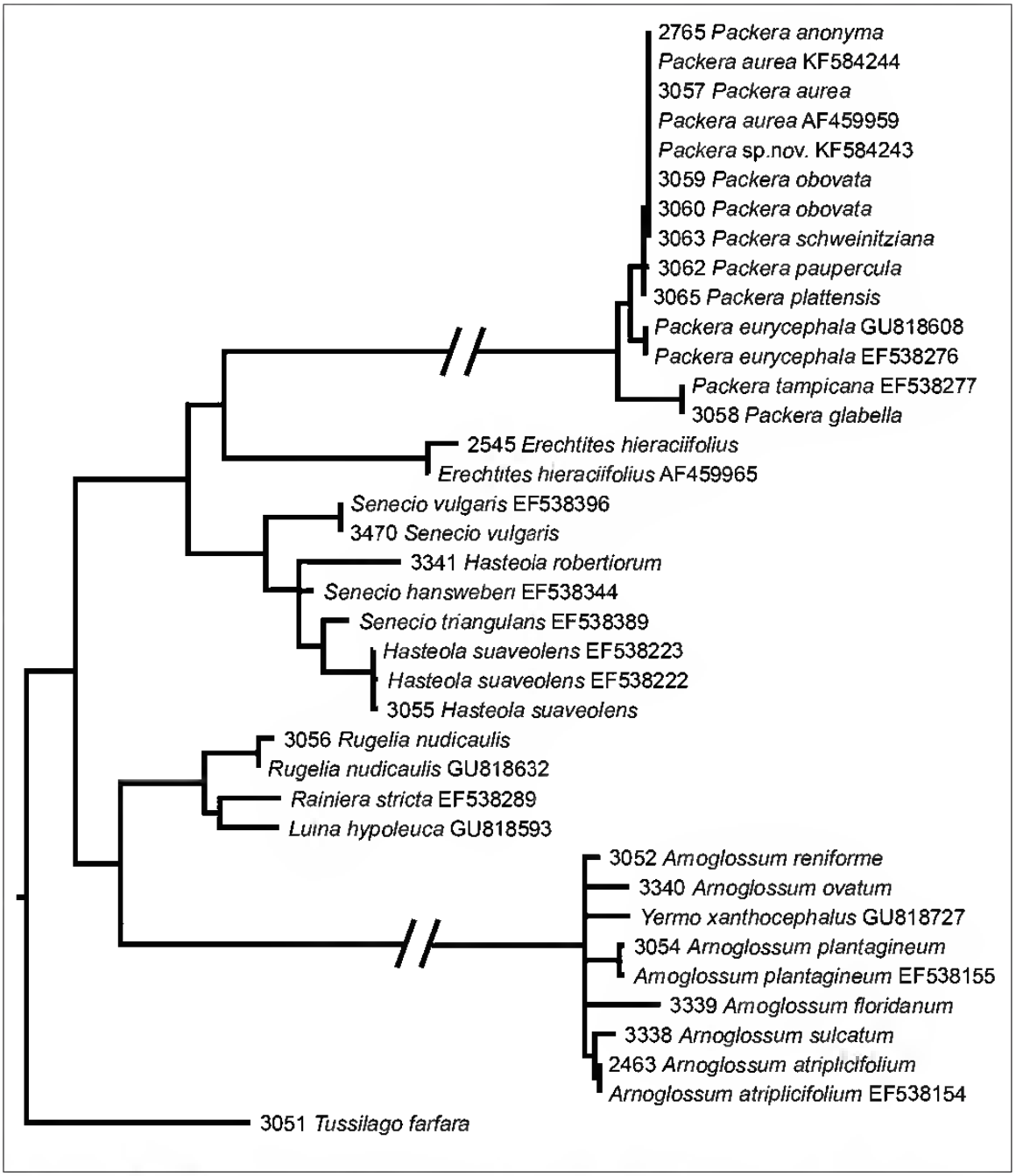

Figure 1. Maximum likelihood bootstrap tree (500 replicates) showing relationships of species of Senecioneae based on ITS sequence data, using *Tussilago farfara* as the root. Newly obtained sequences designated by DNA number preceding species name (Table 1), GenBank numbers for other sequences follow species name.

Materials and Methods

DNA was extracted from leaf samples either collected fresh or taken from herbarium specimens (Table 1). DNA extraction, PCR amplification, and sequencing protocols followed Schilling and Floden (2012). A sample that had a length polymorphism in the ITS region was

sequenced with multiple primers to allow "clean" sequence to be obtained from each direction up to the site of the polymorphism. GenBank accession numbers are provided in Table 1. Although this study was not designed to undertake a rigorous phylogenetic analysis, maximum likelihood analyses using the MEGA5 program (Tamura et al. 2011) were utilized to provide comparative visualization of the sequence results. The resulting tree was rooted using the sample of the introduced *Tussilago farfara*, based on results of Pelser et al. (2007, 2010). The analysis also incorporated sequences deposited at GenBank of conspecific samples or closely related species.

Results and Discussion

Newly obtained ITS sequences for Senecioneae ranged in length from 623-643 bp. Sequences of *Packera* were mostly 625 bp, but *P. glabella* was 628; sequences of *Arnoglossum* were 637-644 bp; those of *Hasteola* were 640 or 644 bp. Only a single species was observed to have a length polymorphism in the ITS region, *H. suaveolens*, in which there was a 2 bp indel that varied between copies. The number of positional polymorphisms (inferred from a double peak on the sequencing electropherogram) was relatively low for all samples, varying from 0 to 5 in individual samples.

The ITS sequences of the sampled genera of Senecioneae were quite different from one another (Fig. 1). Relative to the designated outgroup, *Tussilago farfara*, the species were placed into about five clades in the consensus ML tree (Fig. 1). The species of *Arnoglossum* formed one clade, within which the rare, monotypic western North American *Yermo* was placed as well as the non-Tennessee species *A. floridanum*, *A. ovatum,* and *A. sulcatum*. Sister to the *Arnoglossum* group was a clade that included *Rugelia nudicaulis*, which was quite distinctive from the other Tennessee species of Senecioneae. *Rugelia* was placed in a clade with two small genera of western North America, *Raimera* Greene and *Luina* Benth., in agreement with the results of Pelser et al. (2010). A third clade included species of *Senecio* and *Hasteola* (Fig. 1). Consistent with results reported by Pelser et al. (2007, 2010), *Hasteola* is phylogenetically embedded within *Senecio*, and its current two species likely should be included within *Senecio*. Besides *H. suaveolens*, which occurs in Tennessee, the only other member of *Hasteola* is the Florida panhandle endemic *H. robertiorum*, and not only was there a significant difference between the two species for ITS sequence, they were not even placed as monophyletic in the ML tree (Fig. 1). A fourth group was formed by the two included samples of *Erechtites,* which was placed as sister to *Packera*, albeit with weak support. All of the species of *Packera* were grouped into a single clade within which *P. aurea* and similar species formed a large polytomy and *P. glabella* was placed with (and almost identical to) *P. tampicana* from western North America.

Within genera with more than one species, there was a conspicuous difference among genera in the amount of interspecific variability. Within *Arnoglossum*, for example, all of the species differed from one another by at least 10 bp (3%). In contrast, the Tennessee species of *Packera*, except for *P. glabella*, were essentially identical to one another for ITS sequence. The lack of differentiation in ITS sequence extended to a sample of *P. plattensis* from Oklahoma, which made it impossible to evaluate whether or not the Appalachian populations formerly assigned to this species are distinct from it. A barcoding approach using ITS sequence data could thus only verify identifications of members of *Packera* to genus.

The striking differences in the amounts of interspecific divergence among the different genera of Senecioneae in the southeastern USA suggest that they have undergone divergence at different time intervals. The large amount of divergence within *Arnoglossum* species, and their apparent close relationship to *Yermo* Dorn from western North America, would be consistent with a relatively long history in southeastern North America; Pelser et al. (2010) dated the divergence of the two genera at ca 1.2–1.3 ma (million years ago). The divergence between *Rugelia* and its sister group from western North America is even older, at about 2.3–2.5 ma (Pelser et al. 2010), suggesting that it occurred at a

different time and possibly route than for *Arnoglossum*. Similarly, the large number of differences in ITS sequence between the two species of *Hasteola* also would be consistent with a relatively old separation, and their relationships within *Senecio* may point to separate arrivals in eastern North America. In contrast the lack of divergence among morphologically distinct species of *Packera* suggests a relatively recent arrival in eastern North America.

The results of BLAST searches in GenBank for members of Senecioneae generally gave a top match to a conspecific sample, if the species had been sampled, and sequences already deposited for species represented in Tennessee generally matched closely if not identically the newly sampled ones. The exceptions included a sample labeled *Erechtites hieracifolius* (EF107652), which differed improbably at almost 30 positions compared to other samples of this species, and a sample labeled *Petasites japonicus* (FJ980332) which gave a nearly identical match to sequences from samples of *Tussilago farfara*; both of these apparently erroneous records stemmed from reports described as studies of Chinese medicinal plants. These results provide further examples to show that GenBank cannot be used uncritically as a reference for comparison of molecular barcoding data.

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Table 1. Plant material used for ITS barcoding studies of Senecioneae. All voucher specimens at TENN

Species	DNA#	Genbank	Voucher info
ARNOGLOSSUM Raf.			
A. atriplicifolium (L.) H. Rob.	2563	KJ418356	*Schilling CF-11*, Unicoi Co., TN
A. plantagineum Raf.	3054	KJ418354	*Estes 3384*, Marshall Co., TN
A. reniforme (Hook.) H. Rob.	3052	KJ418353	*Clements 224*, Franklin Co., TN
Non-Tennessee samples			
A. floridanum (A.Gray) H. Rob.	3339	KJ418358	*Beck 9096*, Putnam Co., FL
A. ovatum (Walter) H. Rob.	3340	KJ418355	*Thomas 107296*, Natchitoches Par., LA
A. sulcatum (Fernald) H. Rob.	3338	KJ418357	*McNeilus 01-349*, Camden Co., GA
ERECHTITES Raf.			
E. hieracifolius (L.) Raf. ex DC.	2545	KJ418341	*Schilling 07-DNA2545*, Knox Co., TN
HASTEOLA Raf.			
H. suaveolens (L.) Pojark.	3055	KJ418351	*Estes 9196*, Wayne Co., TN
Non-Tennessee sample			
H. robertiorum L.C. Anderson	3341	KJ418352	*Kral 64504*, Levy Co., FL
PACKERA Á. Löve & D. Löve			
P. anonyma (Wood) Weber & Á. Löve	2765	KJ418348	*Schilling 08-DNA2765*, Knox Co., TN
P. aurea (L.) Á. Love & D. Love	3057	KJ418347	*Floden 866*, Campbell Co., TN
P. glabella (Poir.) C.Jeffrey	3058	KJ418349	*Deselm 06-04*, Bradley Co., TN
P. obovata (Willd.) Weber & Á. Löve	3059	KJ418345	*Rhinehart s.n. 5/2/2005*, Campbell Co., TN
P. obovata (Willd.) Weber & Á. Löve	3060	KJ418346	*Estes 8742*, Cumberland Co., TN
P. paupercula (Michx.) Weber & Á. Löve	3461	KJ418343	*Shaw et al. 682*, Scott Co., TN
P. schweinitziana (Nutt.) Weber & Á. Löve	3063	KJ418344	*DeSelm 01-067*, Unicoi Co., TN
Non-Tennessee sample			
P. plattensis (Nutt.) Weber & Á. Löve	3065	KJ418342	*Taylor 31314*, Taylor Co., OK
RUGELIA Shuttlew. ex Chapm.			
R. nudicaulis Shuttlew. ex Chapm.	3056	KJ418340	*Phillippe 40488*, Sevier Co., TN
SENECIO L.			
S. vulgaris L.	3502	KJ418350	*Schilling 12-DNA3502*, Knox Co., TN
TUSSILAGO L.			
T. farfara L.	3051	KJ418339	*Floden 250*, Campbell Co., TN

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AJO PEAK TO TINAJAS ALTAS: A FLORA OF SOUTHWESTERN ARIZONA
Part 6. POACEAE – GRASS FAMILY

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ABSTRACT

A floristic account is provided for the grass family as part of the vascular plant flora of the contiguous protected areas of Organ Pipe Cactus National Monument, Cabeza Prieta National Wildlife Refuge, and the Tinajas Altas Region in southwestern Arizona. This is the second largest family in the flora area after Asteraceae. A total of 97 taxa in 46 genera of grasses are included in this publication, which includes ones established and reproducing in the modern flora (86 taxa in 43 genera), some occurring at the margins of the flora area or no long known from the area, and ice age fossils. At least 28 taxa are known by fossils recovered from packrat middens, five of which have not been found in the modern flora: little barley (*Hordeum pusillum*), cliff muhly (*Muhlenbergia polycaulis*), *Paspalum* sp., mutton bluegrass (*Poa fendleriana*), and bulb panic grass (*Zuloagaea bulbosa*). Non-native grasses are represented by 27 species, or 28% of the modern grass flora. No other large family in the region has such a high percentage of non-natives. Buffelgrass (*Cenchrus ciliaris*), fountain grass (*Cenchrus setaceum*), and *Schismus* spp. are invasive species of major concern.

The most diverse grass genera in the flora are *Muhlenbergia* (10 species), *Bouteloua* (6 species), and *Aristida*, *Eragrostis*, *Panicum*, and *Sporobolus* (4 species each). *Eragrostis pectinacea* var. *miserrima* is treated as a synonym of *E. pectinacea* var. *pectinacea* and *Muhlenbergia alopecuroides* (*Lycurus setosus*) as a synonym of *Muhlenbergia phleoides* (*Lycurus phleoides*). The modern, established grass flora includes 49 perennials and 37 annuals or ephemerals, of which 20 are summer or hot-season taxa, 12 winter-spring or cool-season taxa, and 5 are non-seasonal. This floristic treatment includes brief descriptions, illustrations, identification keys, common names (when available in English, Spanish, and the local O'odham language), local and global distributions, fossil records from packrat middens, and specimen citations.

POACEAE – Grass Family

This publication is an account of the grasses as part of the vascular plant flora of the contiguous protected areas of Organ Pipe Cactus National Monument, Cabeza Prieta National Wildlife Refuge, and the Tinajas Altas Region in southwestern Arizona (Fig. 1). This is the sixth

contribution to our flora, published in a series in Phytoneuron and also posted open access on the website of the University of Arizona Herbarium (ARIZ). The first article in this series includes maps and brief descriptions of the physical, biological, ecological, floristic, and deep history of the flora area (Felger et al. 2013a). This flora includes the modern, present-day taxa as well as fossil records from packrat middens. Explanation of the format for the flora is provided in part 3 (Felger et al. 2013c).

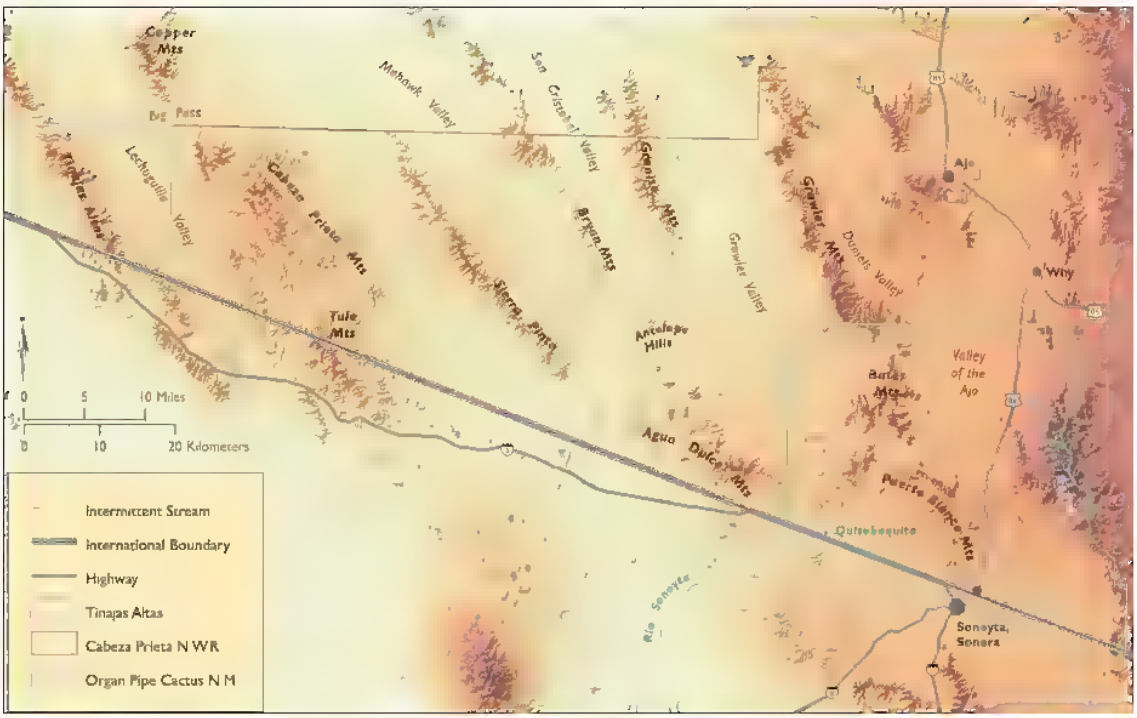

Figure 1. Flora area in southwestern Arizona. Map prepared by Ami Pate of Organ Pipe Cactus NM, 2013

The following generalized descriptions include the grasses in the flora area and not necessarily the same grasses in other regions. There are many variations and not all can be covered in this brief description.

Annual/ephemeral and perennial herbs and some reed- or bamboo-like (*Phragmites*). Roots fibrous; rhizomes and stolons sometimes present. Culms hollow between the nodes and solid at nodes, or less often also solid between the nodes. Leaves basal or cauline (on the culm), 2-ranked, consisting of the sheath, ligule, and blade. Leaf sheaths are partially to fully enclosing the stem, and either open (margins overlapping, not fused) or closed (margins fused). Junction of the leaf sheath and blade called the collar, usually with a ligule, often a scale-like or hairy extension at the top of the leaf sheath and blade and facing the culm (membranous throughout, membranous at the base and topped by cilia, or entirely of hairs). Leaf blades linear with parallel veins, flat or variously folded or inrolled (involute).

In grasses there are several kinds of stems, including culms, rhizomes, and stolons. Technically, "stem" is a general term that can be applied to all of these. The aerial stem of a grass is termed a culm. Inflorescences generally are terminal, sometimes on lateral branches from the culm. (Measurements for culms therefore do not include inflorescences.)

Flowers small, bisexual, or unisexual and the plants monoecious or dioecious. Flowers in spikelets. Terminology for grass inflorescences treats the spikelet as the basic unit in the way the flower is treated in general terminology for flowering plants. Spikelets are in spikes, panicles, or rarely racemes. Panicle branches may be racemose (spikelets with pedicels), spicate (spikelets sessile), or rames (spikelets in pairs, one sessile, one pedicellate), or unilateral (spikelets all on one side of the branch) or not. Spikelets of bracts and 1 or more florets, the bracts and floret(s) 2-ranked (alternate on opposite sides of the rachilla). Bracts variously awned or not; lowermost bracts (glumes) paired or sometimes reduced to 1. The floret includes 2 bracts, the lemma below and the palea above, these enclosing the actual flower (the palea sometimes reduced or absent). In spikelets of more than one floret the lowermost or uppermost floret or florets sometimes staminate or reduced and sterile. Perianth segments (lodicules) of greatly reduced scales, mostly 2 (3 in *Aristida* and *Pappostipa*), often swelling and spreading the floret open at anthesis, or sometimes absent. Pistil single, superior (of 3 united carpels, but functionally with 1 carpel containing 1 ovule). Stamens usually 3, sometimes 1 or 2. Stigmas generally 2 and feathery (plumose). Fruits of specialized achenes (1-seeded) called a caryopsis (caryopses, plural), where the seed is fused to the fruit wall (pericarp), or an actual achene in which the seed separates from the pericarp (*Dactyloctenium* and *Sporobolus*). The caryopsis (including the tightly enclosing fertile lemma and palea in panicoids) or the achene is conveniently referred to as the "grain."

Some grasses, including species of *Bromus*, *Festuca*, and *Sporobolus*, produce mostly or only cleistogamous florets. These are florets that remain closed and produce seeds without exposing the stamens and stigmas and thus are self-fertilized. Cleistogamous grasses tend to occur in dry areas with erratic rainfall, sparse vegetation, and lighter soils (Lord 1981). Five grasses in the flora area produce cleistogenes at the stem bases or in leaf axils: *Cottea pappophoroides*, *Disakisperma dubium*, *Enneapogon desvauxii*, *Muhlenbergia appressa*, and *M. microsperma*. The cleistogenes are modified cleistogamous inflorescences or spikelets, lacking glumes and awns, and the grain is typically larger (heavier) than the grain from "normal" (chasmogamous) florets. Cleistogenes provide a reproductive strategy in addition to that of the usual terminal (chasmogamous) inflorescences, such as when those inflorescences are lost to herbivores or do not develop due to drought.

Grasses in the flora area are distributed among six subfamilies following the classification in Soreng et al. (2013) and the Grass Phylogeny Working Group (2012):

Subfamily Aristidoideae: *Aristida*
Subfamily Arundinoideae: *Phragmites*
Subfamily Danthonioideae: *Schismus*
Subfamily Chloridoideae:
  Tribe Eragrostideae:
    Subtribe Cotteinae: *Cottea*, *Enneapogon*
    Subtribe Eragrostidinae: *Eragrostis*
  Tribe Zoysieae:
    Subtribe Sporobolinae: *Sporobolus*

Tribe Chlorideae:
  unplaced genus: *Dactyloctenium*
  Subtribe Boutelouinae: *Bouteloua*

Subtribe Eleusininae: *Chloris*, *Cynodon*, *Dinebra*, *Diplachne*, *Disaktsperma*, *Leptochloa*
Subtribe Hilariinae: *Hilaria*
Subtribe Gouiniinae: *Tridentopsis*
Subtribe Monanthochloinae: *Distichlis*
Subtribe Muhlenbergiinae: *Muhlenbergia*
Subtribe Pappophorinae: *Pappophorum*
Subtribe Scleropogoninae: *Dasyochloa*
Subfamily Panicoideae
Tribe Paniceae
Subtribe Anthephorinae: *Digitaria*
Subtribe Boivinellinae: *Echinochloa*
Subtribe Cenchrinae: *Cenchrus*, *Setaria*, *Zuloagaea*
Subtribe Melinidinae: *Eriochloa*, *Urochloa*
Subtribe Panicinae: *Panicum*
Tribe Paspaleae: *Hopia*, *Paspalum*
Tribe Saccharеae
Subtribe Anthistiriinae: *Heteropogon*
Subtribe Sorghinae: *Bothriochloa*, *Sorghum*
Subtribe Tripsacinae: *Zea*
Subfamily Pooideae
Tribe Bromeae: *Bromus*
Tribe Hordeeae
Subtribe Hordeinae: *Elymus*, *Hordeum*
Subtribe Triticinae: *Triticum*
Tribe Meliceae: *Melica*
Tribe Poeae
Subtribe Agrostidinae: *Polypogon*
Subtribe Aveninae: *Avena*
Subtribe Poinae: *Poa*
Subtribe Loliinae: *Festuca*
Subtribe Phalaridinae: *Phalaris*
Tribe Stipeae: *Pappostipa*

Spikelets in the subfamily Panicoideae are generally paired (sometimes in triplets on terminal branchlets), the members of a unit usually with pedicels of different lengths or one spikelet sessile, or reduced, or sometimes absent. The individual spikelets detach below the glumes and have 2 florets, the lower one staminate or sterile, often reduced to just a lemma, the upper floret usually bisexual. Many other grasses have spikelets with 2 florets, but rarely have the lower floret staminate or sterile and the upper one bisexual. Two major kinds of spikelets are notable among the subfamily Panicoideae, the andropogonoid and the panicoid spikelets.

Andropogonoid spikelets are seen in *Bothriochloa*, *Heteropogon*, and *Sorghum* in the tribe Saccharеae. There is a basic pattern, but a daunting array of variation. The spikelets are in pairs (triplets often at branch tips—the descriptions that follow are for the paired spikelets). The pairs have 1 sessile/subsessile spikelet and 1 stalked (pedicelled) spikelet. Among those in the flora area the pedicelled spikelet is smaller than the sessile/subsessile one or reduced or absent. The sessile/subsessile spikelet has a staminate or sterile (reduced) floret below and a bisexual or pistillate floret above. The spikelet pair or unit falls with its rachis segment as the dispersing unit. A branch of the inflorescence with such pairs of sessile and pedicelled spikelets is called a rame.

In the panicoids the spikelets in an inflorescence are similar to each other and may be paired or not; pedicels of paired spikelets are of different lengths or one is sessile. What often appears to be a spikelet with one floret is actually a spikelet with two florets. Like the andropogonoids, the lower floret is staminate or sterile, and most panicoid plants in the flora area have the sterile floret reduced to a just a lemma. The sterile lemma generally resembles the upper glume. The upper floret is bisexual, with a lemma, palea, stamens, and pistil. Panicoid spikelets are seen in *Cenchrus*, *Digitaria*, *Echinochloa*, *Eriochloa*, *Panicum*, *Setaria*, *Urochloa*, and *Zuloagaea* in Paniceae and *Hopia* and *Paspalum* in Paspaleae. In *Eriochloa* the lower glume is modified as a cup-like structure. The panicoid spikelets in *Cenchrus* are hidden in burs or fascicles. Others, such as *Hopia*, *Panicum*, and *Urochloa*, have a hard, smooth and shiny fertile lemma with inrolled margins tightly clasping the palea and enclosed fruit.

DIVERSITY, DISTRIBUTION, AND NATURAL HISTORY

The grass flora of the region is large and diverse (Table 1). Grasses established and reproducing in the modern flora include 86 taxa in 43 genera, which is 12% of the total modern flora of approximately 740 taxa (Felger et al. 2013a, b). Poaceae is the second largest plant family in the flora, following the composites (Asteraceae, 112 taxa). At least 28 species of grasses are represented by fossil specimens, 5 of which are no longer present in the flora area. Non-native grasses include 27 species. We also include some modern grasses documented for flora area but not established or reproducing or apparently no longer present and found at the margins of the area. A total of 97 taxa in 46 genera are included in this publication. Organ Pipe Cactus National Monument (OP, or Organ Pipe) supports a modern grass flora of 79 taxa including 24 non-natives; Cabeza Prieta National Wildlife Refuge (CP, or Cabeza Prieta) has a modern flora of 50 taxa including 18 non-natives, and the Tinajas Altas Region (TA, Tinajas Altas) has 18 species including 4 non-natives. The most diverse grass genera in the flora are *Muhlenbergia* (10 species), *Bouteloua* (6 species), and *Aristida*, *Eragrostis*, *Panicum*, and *Sporobolus* (4 species each).

Aristida californica var. *californica* and *Cenchrus palmeri* are essentially endemic to the Sonoran Desert but also extend southward into thornscrub in northwestern Sinaloa, Mexico. Thus, although grasses are successful in the flora area as well as in the Sonoran Desert as a whole, there is no endemism in the flora area and few endemics within the Sonoran Desert (Felger 2000, 2007; Gould & Moran 1980; Malusa et al. 2013; Pearlstein et al. 2012).

Non-native grasses are represented by 27 species, or 28% of the total grass flora (97 taxa), in contrast to 11% non-natives in the total vascular plant flora. No other large family in the region has such a high percentage of non-natives. The non-natives are largely from the Old World and tend to annuals found in disturbed habitats. Six Old World grasses are widespread and common even in undisturbed, natural habitats: red brome (*Bromus rubens*), Bermuda grass (*Cynodon dactylon*), stink grass (*Eragrostis cilianensis*), wild barley (*Hordeum murinum*), and Arabian and Mediterranean grasses (*Schismus arabicus* and *S. barbatus*). Buffelgrass (*Cenchrus ciliaris*), fountain grass (*C. setaceum*), and *Schismus* spp. are invasive species of major concern. Others, such as soft-feather pappus grass (*Enneapogon cenchroides*) and Lehmann love grass (*Eragrostis lehmanniana*) are potentially serious invasives in the flora area. See discussion of non-native and invasive species in the introduction to this flora series in Felger et al. (2013a) and also Felger (1990, 2000) and Felger et al. (2007a).

Table 1. Local distributions and growth forms of grasses. † = modern taxon also represented by a fossil specimen. †† = fossil taxon not found in the modern flora area. * = non-native and reproducing in the flora area. ** = non-native and not established (not reproducing) in the flora area. OP = Organ Pipe Cactus National Monument, CP = Cabeza Prieta National Wildlife Refuge, TA = Tinajas Altas Region. Growth forms: PR = perennial, NS = non-seasonal annual/ephemeral, S = summer or hot-season annual/ephemeral, W = winter-spring or cool-season annual/ephemeral. Totals are for the modern, established flora.

Taxon	Region			Growth form			
	Organ Pipe	Cabeza Prieta	Tinajas Altas	Perennial	Non-seasonal	Summer	Winter
†Aristida adscensionis	OP	CP	TA		NS		
Aristida californica var. californica		CP		PR			
Aristida californica var. glabrata	OP			PR			
†Aristida purpurea var. nealleyi	OP	CP	TA	PR			
Aristida purpurea var. parishii	OP	CP		PR			
Aristida purpurea var. purpurea	OP			PR			
Aristida ternipes var. gentilis	OP	CP		PR			
Aristida ternipes var. ternipes	OP	CP		PR			
*Avena fatua	OP						W
†Bothriochloa barbinodis	OP	CP	TA	PR			
†Bouteloua aristidoides	OP	CP	TA			S	
Bouteloua barbata var. barbata	OP	CP	TA			S	
Bouteloua barbata var. rothrockii	OP			PR			
(†Bouteloua barbata var.?)	OP		TA				
†Bouteloua curtipendula	OP			PR			
†Bouteloua repens	OP			PR			
†Bouteloua trifida	OP	CP		PR			
Bromus arizonicus	OP	CP					W
*Bromus rubens	OP	CP	TA				W
**Bromus tectorum	OP						W
*Cenchrus ciliaris	OP	CP	TA	PR			
**Cenchrus echinatus	OP					S	
(Cenchrus palmeri)						(S)	
*Cenchrus setaceus	OP	CP		PR			
*Cenchrus spinifex		CP				S	
Chloris virgata	OP	CP				S	
Cottea pappophoroides	OP	CP		PR			
*Cynodon dactylon	OP	CP		PR			
*Dactyloctenium aegyptium	OP					S	
†Dasyochloa pulchella	OP	CP	TA	PR			
†Digitaria californica	OP	CP	TA	PR			
Dinebra panicea	OP	CP				S	
Dinebra viscida		CP				S	

Diplachne fusca ssp. uninervia	OP				NS		
Disakisperma dubium	OP			PR			
Distichlis spicata	OP			PR			
*Echinochloa colona	OP	CP				S	
*Echinochloa crus-galli		CP				S	
Elymus elymoides	OP			PR			
*Enneapogon cenchroides	OP				NS		
Enneapogon desvauxii	OP	CP		PR			
(**Eragrostis barrelieri)	(OP)				(NS)		
*Eragrostis cilianensis	OP	CP	TA			S	
Eragrostis intermedia	OP			PR			
*Eragrostis lehmanniana	OP	CP		PR			
†Eragrostis pectinacea		CP				S	
*Eriochloa acuminata	OP					S	
Eriochloa aristata	OP	CP				S	
†Festuca microstachys	OP						W
†Festuca octoflora	OP	CP	TA				W
†Heteropogon contortus	OP	CP	TA	PR			
Hilaria belangeri	OP			PR			
Hilaria rigida	OP	CP	TA	PR			
Hopia obtusa	OP			PR			
*Hordeum murinum	OP	CP					W
††Hordeum pusillum	OP						W
Leptochloa crinita	OP			PR			
Melica frutescens	OP			PR			
Muhlenbergia appressa	OP						W
Muhlenbergia dumosa	OP			PR			
†Muhlenbergia emersleyi	OP			PR			
†Muhlenbergia fragilis	OP					S	
†Muhlenbergia microsperma	OP	CP	TA		NS		
Muhlenbergia phleoides	OP			PR			
††Muhlenbergia polycaulis	OP			PR			
Muhlenbergia porteri	OP	CP		PR			
Muhlenbergia rigens	OP			PR			
Muhlenbergia tenuifolia	OP			PR			
Panicum alatum		CP				S	
*Panicum antidotale	OP			PR			
†Panicum hallii	OP			PR			
†Panicum hirticaule	OP	CP				S	
Pappophorum vaginatum	OP			PR			
Pappostipa speciosa	OP		TA	PR			
††Paspalum sp.	OP			?			
*Phalaris caroliniana		CP					W

*Phalaris minor	OP	CP					W
Phragmites australis	OP			PR			
**Poa annua	OP						W
†Poa bigelovii	OP	CP					W
††Poa fendleriana	OP			PR			
*Polypogon monspeliensis	OP	CP			NS		
*Polypogon viridis	OP			PR			
*Schismus arabicus	OP	CP	TA				W
*Schismus barbatus	OP	CP					W
†Setaria grisebachii	OP					S	
Setaria liebmannii	OP					S	
†Setaria macrostachya	OP	CP		PR			
*Sorghum halepense	OP	CP		PR			
Sporobolus airoides	OP	CP		PR			
Sporobolus cryptandrus	OP	CP	TA	PR			
Sporobolus flexuosus	OP			PR			
Sporobolus pyramidatus	OP					S	
Tridentopsis eragrostoides	OP			PR			
†Tridentopsis mutica	OP	CP	TA	PR			
**Triticum aestivum	OP						W
Urochloa arizonica	OP	CP				S	
††Zuloagaea bulbosa	OP			PR			
Total established taxa in modern flora area: 86	79	49	18	49	5	20	12
Region and growth form	Organ Pipe	Cabeza Prieta	Tinajas Altas	Perennial	Non-seasonal	Summer	Winter

Grasses in the flora area known from fossil packrat middens include at least 28 species (Table 1). Five species, from the Ajo and Puerto Blanco Mountains, are not known in the modern flora: *Hordeum pusillum*, *Muhlenbergia polycaulis*, *Paspalum* sp., *Poa fendleriana*, and *Zuloagaea bulbosa*. *Paspalum* is a wetlands grass and the nearest modern occurrences are near the Colorado and Gila Rivers. The nearest modern occurrences of the other four are mostly at elevations above the desert, such as the Baboquivari and Coyote Mountains. The fossil records indicate wetter ice age conditions. The fossils were identified by fragments of the inflorescences and reproductive structures that often included spikelets or even spikes or spikelet clusters, florets, caryopses or "grain," or combinations or pieces of these parts (see Felger et al. 2013a).

Non-native plants established as reproducing populations in the flora area are indicated with an asterisk (*) and non-native taxa not established as reproducing populations are marked with two asterisks (**). Fossil specimens and modern taxa also represented by fossils are indicated with a dagger symbol (†) and fossil taxa no longer known to occur in the flora are indicated with two dagger symbols (††).

Grasses dominate some high elevation, north-facing slopes of the Ajo Mountains. Relatively few excursions have documented these grasslands due to their remoteness and difficulty of access,

especially during the summer season. Additional explorations are likely to produce new records. At least 58 taxa of grasses occur in the Ajo-Diablo Mountain complex (Felger et al. 2013a). Within the flora area 18 species are known only from the Ajo–Diablo Mountain complex, and *Bouteloua barbata* var. *rothrockii* is known elsewhere in the flora area only from the Bates Mountains. These grasses, listed below, generally extend no farther into the desert and are like sky island populations.

Bouteloua barbata var. *rothrockii*
Bouteloua curtipendula
Elymus elymoides
**Enneapogon cenchroides*
Eragrostis intermedia
Festuca microstachys
Hilaria belangeri
Melica frutescens
Muhlenbergia appressa
Muhlenbergia dumosa
Muhlenbergia emersleyi
Muhlenbergia fragilis
Muhlenbergia phleoides
Muhlenbergia rigens
Muhlenbergia tenuifolia
Pappophorum vaginatum
Setaria grisebachii
Setaria liebmannii
Tridentopsis eragrostoides

Perennial grasses in the established modern flora are represented by 49 taxa (Table 1). However, many or perhaps most of these perennials can be reproductive in the first year or season. Several perennials are not truly herbaceous, e.g., *Hilaria rigida*, *Muhlenbergia dumosa*, and *Phragmites australis*. Annuals (ephemerals) are represented by 37 taxa, summer ephemerals by 20 taxa, cool-season or winter-spring ephemerals by 12 taxa, and non-seasonal ephemerals include 5 species.

Seven species, only two of them native, are restricted to wetland habitats, which are often characterized by highly alkaline or saline soils. *Phragmites australis* and **Polypogon viridis* are highly localized and limited to habitats with permanent water. The others are *Distichlis spicata*, **Echinochloa colona*, **E. crus-galli*, ***Poa annua*, and **Polypogon monspeliensis*.

Five grasses are common on the dunes of the Pinta Sands and nearby sand soils and interdune troughs: *Aristida californica* var. *californica*, *Bouteloua aristidoides*, *B. barbata* var. *barbata*, *Hilaria rigida*, and **Schismus arabicus*. However, all occur elsewhere although *A. californica* var. *californica* is mostly restricted to sandy soils.

Following years of favorable rains in late summer and early fall, extensive ephemeral grass-dominated meadows may develop on certain low-lying habitats, such as the large playas and sandy loams of the lower bajadas. Characteristic grasses in these places include *Aristida adscensionis*, *Bouteloua aristidoides*, *B. barbata* var. *barbata*, *Chloris virgata*, *Dinebra* (*Leptochloa*) *panicea*, *Dinebra* (*Leptochloa*) *viscida*, **Eragrostis cilianensis*, *Eriochloa aristata*, *Muhlenbergia microsperma*, *Panicum alatum*, and *P. hirticaule*.

Sandy plains in the northern part of Organ Pipe provide favorable conditions for grasses—in particular lower bajada and floodplain deposits of sandy loams along flat reaches of drainages in the Valley of the Ajo. In fact this area has the highest concentration of grass species known for the region. This dense growth of grasses supports large rodent populations, so that during years of favorable rainfall it is best to wear legging as protection from the numerous unseen rattlesnakes that feed on the rodents (Phil Rosen, pers. comm. to R. Felger 2006). In this area 21 grasses have been recorded in less than one hectare:

Aristida adscensionis
Aristida purpurea var. *nealleyi*
**Eragrostis cilianensis*
Festuca octoflora

Bouteloua aristidoides
Bouteloua barbata var. *barbata*
Bromus arizonicus
**Bromus rubens*
Cottea pappophoroides
Dasyochloa pulchella
Digitaria californica
Dinebra panicea
Eriochloa aristata
Hilaria rigida
Muhlenbergia microsperma
Muhlenbergia porteri
Panicum hirticaule
Poa bigelovii
**Schismus barbatus*
Setaria macrostachya
Sporobolus flexuosus

Economic grasses have played an important role in regional agriculture and food resources. Maize (*Zea mays*) has been cultivated in the region since prehistoric times. In 1701, Padre Kino and his companions found O'odham people cultivating maize (corn) along the river at Sonoyta (Burrus 1971) and brought wheat (*Triticum aestivum*) and other crops to the area (Bolton 1919). The missionaries also introduced cattle, which thrived on grasses and other forage, which undoubtedly contributed to the ultimate demise of some local grasses and wetland habitats (Felger 2000, 2007).

Most grasses produce edible grain. Native Americans in the flora area harvested grain from grasses that was large enough and/or abundant enough to make the effort worthwhile. Even those with very small grain were harvested for food by Sonoran Desert people, including the annual grama grasses (e.g., *Bouteloua aristidoides*) and even little-seed muhly (*Muhlenbergia microsperma*) and many perennials such as bull grass (*Muhlenbergia emersleyi*). Although these and other common grasses have very small grains, they can be so abundant that significant quantities could be collected in a relatively short time. Others have substantially larger and perhaps more readily harvested and prepared grain, such as vine mesquite (*Hopia obtusa*), plains bristlegrass (*Setaria macrostachya*), and alkali sacaton (*Sporobolus airoides*). These grains were often basket winnowed to separate chaff, parched, ground into flour, and cooked or stored for later used. The flour was mixed with other foods or consumed as porridge. Pertinent references include Castetter (1935), Castetter and Bell (1942, 1951), Castetter and Underhill (1935), Childs and Dobyns (1954), Felger (2007), Felger and Moser (1985), Felger et al. (1992), Gasser (1982), Hodgson (2001), Lumholtz (1912), and Rea (1997).

KEY TO THE GRASS GENERA OF SOUTHWESTERN ARIZONA

In the various keys we make use of annual (ephemeral) vs. perennial growth forms mainly in an attempt to produce keys as user-friendly as possible. The drawback is that many or most of the perennials may, on occasion, become reproductive in their first year or season. Even so, these occasional first year/season plants generally have more extensive root systems than the truly annual/ephemeral grasses, and in such cases perennial individual plants are generally far more numerous than the occasional first season/annual individuals. We use the terms ephemeral and annual almost interchangeably and nearly all annual grasses in the flora area are ephemerals, although ephemerals are plants that can grow and mature in a single season, while annuals are longer lived but not perennial. In the descriptions and keys, we also are not always consistent in using singular and plural nouns for part of plants (plural is usually implied), e.g., spikelet vs. spikelets.

The keys and following descriptions pertain to grasses occurring in the flora area and may not cover the variation found in other regions. The descriptions are meant to be informative, brief, and tailored for grasses in the flora area and are not necessarily of consistent detail for the different taxa. More detailed descriptions are available in many other sources such as the Manual of Grasses for North America (Barkworth et al. 2007a) and the Flora of North America (Barkworth et al. 2003, 2007b). Our keys do not include the fossils.

1. Plants bamboo- or reed-like, 1–3 m tall.

    2. Plants mostly 1–1.5 m tall; leaf blades not more than 12 cm long, less than 0.5 cm wide; spikelets with 1 floret; Ajo Mountains..... **Muhlenbergia dumosa**
    2. Plants mostly more than 2 m tall; leaf blades (7) 30–40 cm long, more than 1 cm wide; spikelets several florets; vicinity of Quitobaquito..... **Phragmites australis**

1. Plants not bamboo or reed-like.

    3. Plants with stolons and/or rhizomes; perennials.

        4. Plants creeping and/or forming dense colonies or mats, the rhizomes or stolons creeping and scaly; spikelets awnless; often in riparian or weedy habitats, or saline or alkaline soils.

            5. Inflorescence a panicle of digitately arranged branches; spikelets, 2–2.5 mm long, with 1 floret..... **Cynodon dactylon**
            5. Inflorescences of compact racemes or panicles, not digitately arranged; spikelets 1.4–15 mm long, with 1 to several florets.

                6. Spikelets with several florets; glumes 2.7–4.5 mm long, the lemmas 3–5 mm long. ..... **Distichlis spicata**
                6. Spikelets with 1 floret; glumes 1.4–2.1 mm long, the lemmas 0.8–1 mm long. ..... **Polypogon viridis**

        4. Plants tufted, with short or long stolons or rhizomes, these not scaly, not creeping, and not mat forming; spikelets awned or awnless; often in open, desert habitats.

            7. Inflorescence spike-like and elongated, less than 1.5 cm wide (and more than 4 cm long).

                8. Stolon less than 20 cm long; spikelets awned, in clusters of 3's..... **Hilaria**
                8. Stolons to 1+ m long; spikelets awnless, not in 3's..... **Hopia obtusa**

7. Inflorescences various, dense or open panicles, mostly more than 2 cm wide, not elongated and spike-like.

9. Stems often 1–2 m tall; inflorescences of open panicles often more than 10 cm wide; spikelets awnless..... **Panicum antidotale**
9. Stems less than 40 cm tall; inflorescences or their branches with spikelets crowded, less than 3 cm wide; spikelets awned.

10. Plants 8–40 cm tall; flowering stems more than twice as tall as the leaves; inflorescence a panicle of spicate, unilateral branches, 1 to several widely spaced on the flowering stem..... **Bouteloua trifida**
10. Plants less than 15 cm tall; flowering stems less than twice as tall as the leaves; inflorescence a dense panicle of spicate but not unilateral branches ..... **Dasyochloa pulchella**

3. Plants without conspicuous stolons or rhizomes; annuals (ephemerals) or perennials.

11. Spikelets subtended by 1 or more bristles or enclosed in burs or fascicles.

12. Spikelets enclosed in burs or fascicles with many spines or bristles, the bur or fascicle falling as a unit with the attached spines or bristles..... **Cenchrus**
12. Spikelets not enclosed in burs or fascicles, with 1–few slender bristles below the spikelets; spikelets breaking off above the bristles..... **Setaria**

11. Spikelets not subtended by bristles and not enclosed in burs or fascicles.

13. At least some spikelets with awns.

14. Spikelets or some or all florets with 3 terminal awns from a common point or central column.

15. Inflorescences panicles of spicate, unilateral branches; spikelets with 2-several florets including rudiments; awns 8 mm or less in length..... **Bouteloua**
15. Inflorescences panicles of racemose branches, not unilateral; awns 12 or more mm long.

16. Spikelets clearly with 1 floret with 1 or 3 awns..... **Aristida**
16. Spikelets with 2 florets, 1 fertile and 1 sterile, each with 3 awns. ..... **Leptochloa crinita**

14. Spikelets with 1 or more awns, but not 3-awned as above.

17. Perennials, almost always obviously so with well-developed root systems.

18. Lemmas with 7 or more scabrous or feathery awns.

19. Plants not forming cleistogenes; glumes with 1 prominent vein. ..... **Pappophorum vaginatum**
19. Plants forming cleistogenes at stem bases; glumes with 5–13 veins (not the cleistogene spikelets).

20. Panicles open and diffuse; glumes with 7–13 veins; lemma with 9 or more scabrous awns (not feathery)…….. **Cottea pappophoroides**
20. Panicles contracted and dense; glumes with 5–7 veins; lemmas with 9 feathery awns…….. **Enneapogon**

18. Lemmas with 1 to several awns.

21. Plants less than 15 cm tall; leaves fascicled….. **Dasyochloa pulchella**
21. Plants usually more than 20 cm tall; leaves not conspicuously fascicled.

22. Awns 2 or more cm long.

23. Awns several per spikelet, scabrous, straight or moderately curved but not bent…….. **Elymus elymoides**
23. Awns one per spikelet, feathery or twisted at base, and bent.

24. Older leaves semi-persistent and reddish brown or rust colored; inflorescences unbranched (rames); awns 4.5–7 cm long. …… **Heteropogon contortus**
24. Older leaves drying straw color; inflorescences branched (panicles); awns 2–4.5 cm long.

25. Inflorescence a panicle of short cottony rames clustered near top of stem; awns 2 cm long, the basal portion twisted and not feathery…….. **Bothriochloa barbinodis**

25. Inflorescence an elongated spike-like panicle and not cottony; awns 3.3–4.5 cm long, the basal portion feathery (plumose) and not twisted…….. **Pappostipa speciosa**

22. Awns less than 1.5 (2) cm long.

26. Inflorescence spike-like, appearing unbranched, less than 1.5 cm wide, the main axis zigzag; spikelets in clusters of 3…… **Hilaria**
26. Inflorescence a panicles, the main axis not zigzag, usually more than 1.5 cm wide; spikelets solitary, or in 2's (terminal spikelets sometimes in 3's).

27. Plants bushy, not tufted, branching freely in upper part of plant; panicles about as wide as long…... **Muhlenbergia porteri**
27. Plants tufted, branching mostly from base (not including the inflorescences); panicles usually longer than wide.

28. Spikelets dissimilar, in 2's (3's terminally on branchlets); awns twisted and readily deciduous…... **Sorghum halepense**
28. Spikelets all similar, not as above; awns persistent, not twisted.

29. Spikelets with 1 floret; awns more than 10 mm long. …….. **Aristida ternipes** var. **ternipes**

29. Spikelets with several florets; awns less than 0.5 mm long..... **Tridentopsis eragrostoides**

17. Ephemerals (roots often weakly developed)/annuals.

30. Spikelets clustered in 3's; glumes bristle-like..... **Hordeum murinum**
30. Spikelets not clustered in 3's; glumes not bristle-like.

31. Spikelets (excluding awns and pedicels) at least 10 mm long (rarely 8 or 9 mm long in *Festuca*), clearly with 2 or more florets; winter-spring ephemerals.

32. Glumes thin and longer than the florets (excluding awns), the glumes and lemmas of different textures; awns twisted and bent, 3.5–4.5 cm long..... **Avena fatua**
32. Glumes shorter than the spikelet and similar in texture to the lemmas; awns straight or twisted and bent, 2.2 cm or less in length.

33. Sheaths closed most of their length; spikelets 12–40 mm long (not including awns); lemmas 8–13 mm long; awns straight, curved, or twisted..... **Bromus**
33. Sheaths open; spikelets 8–13 mm long (not including awns); lemmas 4–8 mm long; awns straight..... **Festuca**

31. Spikelets (excluding awns and pedicels) 2–6 (7) mm long, with 1–several florets; winter-spring or summer ephemerals.

34. Inflorescences panicles of spicate, unilateral branches.

35. Inflorescence branches single at intervals along main inflorescence axis (occasional, stunted plants with a single branch).

36. Awns 6 mm or less in length; sterile florets above fertile florets, the sterile lemmas minute; desert habitats, widespread.... **Bouteloua**
36. Awns often more than 10 mm long; sterile floret below the fertile floret, the sterile lemma equal to upper glume and fertile lemma; wetland habitats or moist soil..... **Echinochloa crus-galli**

35. Inflorescence branches 2 or more digitately arranged at top of main axis (rarely a single spike on stunted *Dactyloctenium* plants).

37. Spicate branches (4) 5–10 (12 or more) and ascending (upright); rachis tip not extending beyond spikelets; spikelets (lemma of lower floret) with a tuft of long white hairs, the awns 5–20 mm long. ..... **Chloris virgata**
37. Spicate branches (rarely 1) 2–6, spreading (at nearly right angles to main axis); rachis tip extending beyond the spikelets; spikelets glabrous, the awns 0.5–3.2 mm long.... **Dactyloctenium aegyptium**

34. Inflorescences not panicles of spicate, unilateral branches.

38. Spikelets with a conspicuous basal cup-like or disk-like ring, with only one well-developed glume…….. **Eriochloa**
38. Spikelets without a basal cup or disk, with 2 glumes.

39. Spikelets with several fertile florets; awns 1 mm long …….. **Dinebra viscida**
39. Spikelet with only 1fetile floret; awns at least 5–10 mm long.

40. Panicles dense, more or less cylindrical and appearing "furry" like a rabbit's foot…….. **Polypogon monspeliensis**
40. Panicles open or interrupted with spike-like branches, not appearing "furry."

41. Coarse grasses with dense spike-like branches at widely spaced intervals on a main axis; fertile lemmas hard and shiny; cleistogenes none; natural and disturbed wetland habitats. …….. **Echinochloa crus-galli**
41. Delicate grasses with open and filmy panicles; lemmas thin and dull; lower stem axils commonly with cleistogenes; widespread including desert habitat. …….. **Muhlenbergia microsperma**

13. Spikelets not awned (sometimes with minute bristles or mucros).

42. Non-seasonal ephemerals to perennials; spikelets with 1 floret, 1.4–2.1 mm long, with a pedicel-like stipe; glumes longer than the florets and minutely scabrous; lemmas 5-veined; Quitobaquito ..... **Polypogon viridis**
42. Spikelets with 1 or more florets, if with a single floret the spikelets larger, and/or not scabrous, and/or the lemmas not 5-veined.

43. Perennials.

44. Spikelets pubescent.

45. Spikelets cottony with silky, white or purplish, usually curling hairs; lower glume less than 1 mm long…….. **Digitaria californica**
45. Spikelets not cottony, sparsely to moderately pubescent, the hairs straight and not silky; lower glume 2+ mm long…….. **Tridentopsis**

44. Spikelets glabrous.

46. Spikelets including the glumes papery and shiny, glumes 7–15 mm long. …….. **Melica frutescens**
46. Spikelets not papery and shiny; glumes not more than 5 mm long.

47. Inflorescences 0.5–1 cm wide, dense, spike-like panicles. …….. **Muhlenbergia rigens**
47. Inflorescences more than 3 cm wide, not dense, spike-like panicles.

48. Cleistogenes often present at stem bases; panicles not enclosed in leaf sheaths; spikelets with 5 or more florets; lemmas 3-veined, notched at tip..... **Disakisperma dubium**
48. Cleistogenes not present stem bases; young panicles often enclosed in a large leaf sheaths, with age usually becoming open and diffusely branched; spikelets with 1-floret; lemmas 1-veined, not notched. ..... **Sporobolus**

43. Ephemerals.

49. Hot weather (summer-fall) ephemerals.

50. Spikelets with only one well-developed glume and a cup-like disk at the base (the glume and sterile lemma are similar)..... **Eriochloa**
50. Both glumes well developed, spikelets without a cup-like disk at base.

51. Spikelets with 2 or more distinct, fertile florets; glumes similar or unequal in length.

52. Primary panicle branches two or more times branched, the secondary branches usually ascending to spreading; pedicels often as long as or longer than the spikelets..... **Eragrostis**
52. Primary panicle branches unbranched, spike-like, or with secondary branchlets closely appressed; pedicels much shorter than the spikelets or spikelets subsessile..... **Dinebra panicea**

51. Spikelets with 1 floret, or superficially appearing to have a single floret (with 1 fertile floret and one reduced floret represented by a sterile lemma); glumes unequal in length, one or both conspicuously shorter than the lemma.

53. Leaves often with purple spots or bands; inflorescences of 3–7 racemosely-arranged, widely spaced, spicate branches 1–2 (3) cm long; spikelets densely crowded..... **Echinochloa colona**
53. Leaves not purple spotted or banded; inflorescences diffuse panicles or contracted and spike-like in immature inflorescences of *Sporobolus*; spikelets pedicellate, not densely crowded.

54. Spikelets 1–1.8 mm long, breaking apart above the glumes; spikelets with 1 floret, lacking a sterile floret; lemma, palea, and caryopsis distinct from each other.

55. Panicle branches alternate (single) or opposite; spikelets 1–1.2 mm long; lemmas 3-veined..... **Muhlenbergia fragilis**
55. Branches at lowest node of panicle whorled with (4) 5 or more branches (concealed by leaf sheath in younger inflorescences); spikelets 1.5–1.8 mm long; lemmas 1-veined. ..... **Sporobolus pyramidatus**

54. Spikelets 2.3–4 mm long, falling as a unit (breaking off below the glumes); spikelets with a fertile and a sterile floret, the sterile

floret represented by a prominent lemma; fertile lemma firmly enclosing the palea and caryopsis.

56. Plants variously hairy but panicle branches, branchlets, and spikelets glabrous; prominent veins of spikelets longitudinal only. ..... **Panicum**
56. Plants hairy, including panicle branches, branchlets and spikelets; prominent veins of spikelets longitudinal and transverse on upper part of spikelet to form a net-like pattern..... **Urochloa**

49. Cool season (winter-spring) ephemerals.

57. Primary panicle branches spreading; prominent large shining yellow, pink, or purplish glandular areas or rings at or below nodes, especially prominent on lower nodes of inflorescences (rare in the flora area)..... **Eragrostis barrelieri**
57. Primary panicle branches appressed or closely ascending; plants without large shining glandular areas or rings.

58. Glumes conspicuously shorter than florets..... **Poa**

58. Glumes longer than the florets.

59. Spikelets with one fertile floret and 1 or 2 scale-like sterile florets below; glumes usually with a winged keel..... **Phalaris**
59. Spikelets with several similar fertile florets, and without sterile florets below the fertile ones; glumes not winged..... **Schismus**

SPECIES ACCOUNTS

This is a specimen-based flora and we have seen or verified all specimens cited. All specimens cited are at the University of Arizona Herbarium (ARIZ) unless otherwise indicated by the abbreviations for herbaria at Cabeza Prieta National Wildlife Refuge (CAB), Organ Pipe Cactus National Monument (ORPI), and the standardized abbreviations for herbaria (Index Herbariorum, Thiers 2013). Vernacular (common) names follow the scientific names or synonyms and when known or deemed worthwhile are given in English, Spanish, and the Hia C-ed O'odham dialect, respectively. The Spanish-language names are italicized.

All photos and scans are by Sue Rutman and all line art is by Lucretia Brezeale Hamilton (1908–1986) unless otherwise stated. The scans were made with fresh specimens. Lucretia's artwork also has appeared in numerous publications, especially ones published by the University of Arizona Press (e.g., Felger 2000, Felger & Moser 1985, Gould 1951, Parker 1972).

Aristida – Three-awn; *zacate tres barbas*

Annuals/ephemerals and perennials, often tufted, without stolons or rhizomes. Ligule a line of hairs. Spikelets with 1 floret, readily breaking off above the glumes (often lodging in socks and fabric shoes, so that people are often dispersal agents along with various animals). Glumes persistent, the upper and usually also the lower glume 1-veined. Lemmas hard at maturity, terete, slender, with a sharp-pointed callus at the base, the lemma apex elongated into a straight or twisted awn column or neck (narrowed part of awn column), the awn column bearing 3 awns, or the lateral awns sometimes reduced or absent, or the awns occasionally suppressed in drought-stressed plants. Figure 2.

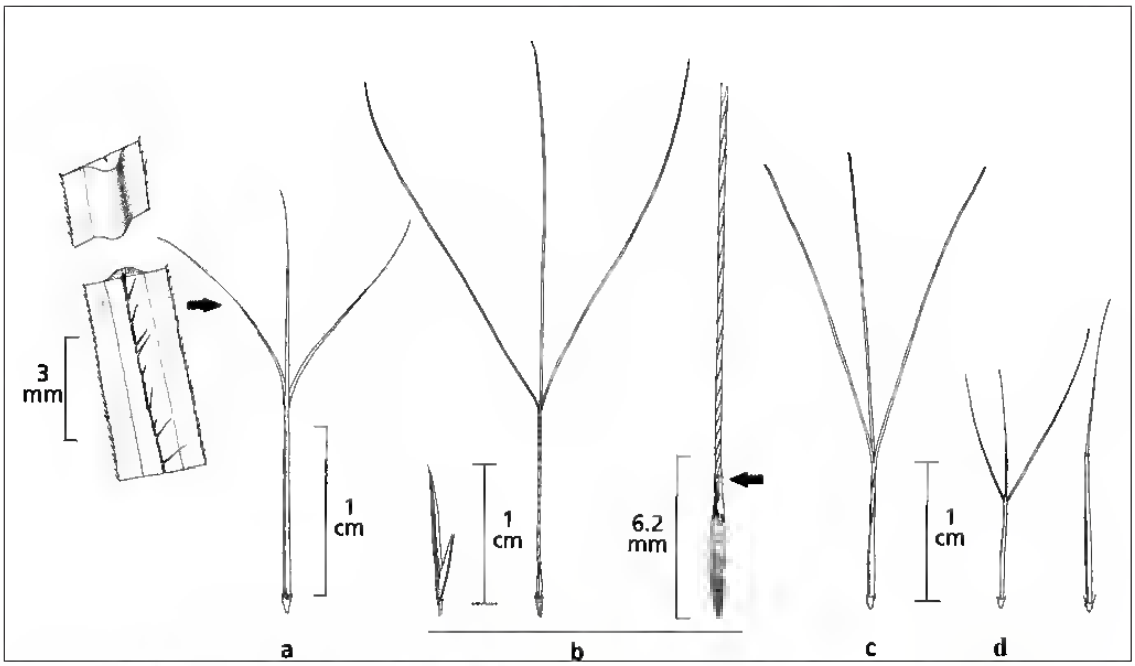

Figure 2. *Aristida* spikelets. (A) *A. adscensionis*, note enlarged portion of flattened awn and minute hairs on the upper surface; (B) *A. californica* var. *californica*, glumes on left, arrow points to the articulation near the base of the long awn column; (C) *A. purpurea* var. *nealleyi*; (D) *A. ternipes* var. *gentilis* (left) and var. *ternipes*. Illustration by Matthew B. Johnson (from Felger 2000).

The four species in the flora region can grow and become reproductive at various seasons depending on soil moisture, although the perennials tend to become inactive with cooler weather in winter and are sometimes reproductive in their first season.

1. Spikelets 1-awned, or lateral awns very short and stubby; perennials. ..... **Aristida ternipes** var. **ternipes**
1. Spikelets 3-awned, the 3 awns usually well developed (if lateral awns reduced, then the plants are stunted ephemerals); ephemerals or perennials.

2. Ephemerals, awns flattened with minutely serrated margins (seen with at least 10× magnification), reaching 1.5 (1.7) cm long (awns occasionally very reduced, especially the lateral ones) ..... **Aristida adscensionis**
2. Perennials (sometimes flowering in the first season), awns terete, (1.6) 2 or more cm long.

3. Awn column of mature spikelets breaking apart at a line of separation (seen as a horizontal line across the column) just above the lemma body, awns 3–5 cm long ..... **Aristida californica**
3. Awn column not jointed, awns (1.6) 2–3 cm long.

4. Panicles open and conspicuously branched, the branches mostly long and spreading at about 90° from the main axis ..... **Aristida ternipes** var. **gentilis**
4. Panicles contracted to moderately spreading, the branches short, mostly spreading at 45° or less ..... **Aristida purpurea**

Aristida adscensionis Linnaeus
Six-weeks three-awn; *zacate tres barbas.* Figure 3.

Non-seasonal ephemerals; 7–30 (60) cm tall, often with a purple-brown cast during cooler, drier seasons and green to yellow-green during summer-fall rainy season; glabrous except very short hairs of the ligule and minutely scabrous pedicels. Roots usually weakly developed. Panicles narrow (contracted), with short erect-ascending branches, or larger well watered plants often with larger and somewhat spreading branches. Glumes unequal: lower glume shorter, the upper glume longer, ranging from shorter to slightly longer than lemma. Lemmas 6.5–10.5 mm (shorter on drought-stressed plants), tapered toward the tip, not twisted; awn column short or with no discernable neck. Awns usually 3, often 5–15 (17) mm long, about equal to unequal in length, flattened (a useful diagnostic character and one of striking beauty seen with at least 10× magnification), the midrib prominent, its upper (adaxial) surface bearing a row of slender hairs 0.5–0.8 mm long; awn margins narrowly winged, thin, translucent, and serrulate. Drought-stressed plants or local populations sometimes with reduced or aborted lateral awns, or all awns reduced or rarely awnless.

Figure 3. *Aristida adscensionis.* (A & C) Little Ajo Mts, Pima Co., 2 Apr 2013; (B) spikelet.

Widespread and seasonally common across the flora area, from lowest to highest elevations, sandy to rocky soils. It has been widespread in the region for at least 32,000 years.

One of the several most widespread and abundant ephemerals of the Sonoran Desert and the only annual (ephemeral) *Aristida* in the Sonoran Desert Region. Warmer regions of the world (Africa, Americas, Eurasia), deserts to relatively humid, tropical and temperate climates. In some non-desert regions plants of this species are short-lived perennials with stout roots.

Worldwide "a number of varieties have been proposed . . . but they intergrade one with another and their significance is doubtful" (Clayton 1972: 372). Beetle (1974) recognized 7 varieties for Mexico, but Felger (2000) and others did not find them worthy of recognition. Recognizing two subspecies worldwide, Tzvelev (1983) restricted subsp. *adscensionis* to the New World and parts of Africa. He reported subsp. *heymannii* in the Old World, distinguished by having the lemma longer than the upper glume and being scabrous only along the keel. However, these features occur on plants from the flora area and elsewhere in the New World. Furthermore, the relative lengths of the lemma and upper glume can vary with age and growing conditions (Allred 2003; Felger 2000).

OP: Bates Well, *Nichol 26 Apr 1939*. Alamo Canyon, 3 Dec 1977, *Bowers 978*. Sierra de Santa Rosa, 11 Feb 1978, *Bowers 1034*. †Alamo Canyon, florets, 8590 to 32,000 ybp (3 samples). †Montezuma's Head, 13,500 to 21,800 ybp (4 samples). †Puerto Blanco Mts, 130 to 7560 ybp (6 samples, Van Devender et al. 1990: 339).

CP: 6 mi E of Papago Wells, 1100 ft, 28 Feb 1976, *McLaughlin, Fugate, & McManus 1037* (SNM). Charlie Bell Pass, 3 Apr 1992, *Whipple 3954*. Bates Well Rd at E boundary of the Refuge, 14 Sep 1992, *Felger 92-681*. San Cristobal Wash, 14 Sep 1992, *Felger 92-690*. Pinta Sands, 1 Feb 1992, *Felger* (observation).

TA: Frontera Canyon, 18 Mar 1998, *Felger* (observation). Tinajas Altas, 25 Oct 2004, *Felger 04-69*. †Butler Mts, 8160 & 10,615 ybp (Van Devender et al. 1990: 342). †Tinajas Altas Mts, 5080 to 10,070 ybp (3 samples, Van Devender et al. 1990: 341).

Aristida californica Thurber

Non-seasonal perennials, readily recognized by the articulated awn column and long, slender awns. Lemmas jointed at the column base (the articulation, visible as a line across the column, is best seen on mature spikelets); awn column relatively long, loosely twisted, relatively slender, often lighter colored than the lemma body. Reproductive at various seasons depending on soil moisture.

Soon after (or sometimes even before) the florets fall away or blow away from the parent plant, the awn column breaks off at the joint just above the body of the lemma, leaving the seed-bearing lower part free from the long awns and thus slowing its movement. The jointed, or articulated, awn column is a distinctive feature of a small group of sand-inhabiting aristidas in widely disjunct regions around the world once regarded as section *Arthratherum* (Henrard 1929–1932), but Cerros-Tlatilpa et al. (2011) clearly show that Henrard's *Arthratherum* is not monophyletic. There is no other *Aristida* in western North America with an articulated awn column. There are two allopatric varieties.

1. Stems pubescent..... **Aristida californica** var. **californica**
1. Stems glabrous..... **Aristida californica** var. **glabrata**

Aristida californica var. **californica**
[*A. peninsularis* Hitchcock. *A. californica* var. *fugitiva* Vasey]
California three-awn; *tres barbas de California*. Figure 4.

Figure 4. *Aristida californica* var. *californica*. Plant with young panicles showing the reddish awns, a common color during cooler and drier months, dunes south of Sierra Blanca, Pinacate Reserve, Sonora, 20 Feb 2002.

Perennials, sometimes flowering in the first season, small tufted clumps overtopped with densely-flowered panicles, often with a red-purple cast during the cooler, drier times of the year and green during summer rainy season. Roots relatively thick, fleshy, well developed, encased in a jacket of sand laced together by a felt-like mat of root hairs. At least the lower stem internodes with fine to coarse white-woolly hairs (note: look at the actual stem, not just the leaf sheath). Upper glume 10.5–17.5 mm long, the lower one shorter. Lemma body (portion below joint of column) (5) 5.5–6 (7) mm long, often gray and mottled; awn column (10) 12–18 (28) mm long, loosely twisted, slender, often lighter colored than the lemma body, awns 3–5 cm long.

Cabeza Prieta on the sand flats and dunes of the Pinta Sands and similar nearby habitats along the southern margin of the Refuge. Also in nearby regions such as the Mohawk Dunes and widespread in the adjacent Gran Desierto.

Southwestern Arizona, southeastern California, both Baja California states, and northwestern Sonora southward on coastal dunes to northwestern Sinaloa.

The roots of this and various other perennial grasses inhabiting desert sands are often encased in a jacket of sand laced together by mucilage and felt-like mats of persistent root hairs. These sheaths of sand grains, or rhizosheaths, create a nano-habitat supporting nitrogen-fixing bacteria (Danin 1996). The rhizosheaths of *Aristida californica* var. *californica* are especially conspicuous and seem best developed during times of high soil moisture (Felger 2000). The Seris fashioned hairbrushes from the wiry roots (Felger & Moser 1985).

CP: Pinta Sands, 590 ft 2*n* = 22, 5 Mar 1977, *Reeder 6835*. Edge of Pinacate Lava and Pinta Sands (8 mi W of O'Neill's Grave), 590 ft, sandy wash, 6 Mar 1977, *Reeder 6838*. E Pinta Sands, 16 Jun 1992, *Felger 92-628*

Aristida californica var. **glabrata** Vasey
[*A. glabrata* (Vasey) Hitchcock]
Smooth California three-awn, Santa Rita three-awn

Plants glabrous, including stems. Sandy loam soils of washes and roadsides in the north-central part of Organ Pipe.

Eastward and northward across much of the southern half of Arizona, northern and west-central Sonora, Isla Tiburón, and both states of Baja California. This variety generally occurs on firmer ground than does var. *californica* and their local ranges do not overlap (Reeder & Felger 1989).

OP: 4 km S of the N entrance of Monument along Hwy 85, localized clumps at edge of road, 27 Oct 1987, *Reeder 8218*. 2.2 mi on Hwy 85 south of N entrance of monument, roadside, 12 Nov 1987, *Felger 87-334* (ARIZ, ASU).

Aristida purpurea Nuttall
Purple three-awn. Figure 5.

Tufted perennials with well-developed fibrous roots. Ligules with a sparse tuft of loosely tangled hairs; leaf blades narrow, firm, inrolled or flat when well-watered during growing seasons, the upper surfaces with short, stiff, somewhat scabrous hairs. Panicles overtopping the leaves. Glumes usually unequal. Lemmas with or without a conspicuous neck (column), but shorter than 3 mm; awns about equal in length. Flowering response non-seasonal.

Aristida purpurea including its varieties extends from Mexico through western USA to Canada. Allred (1984, 2003) recognized 10 varieties in North America, and other members of the complex occur in South America.

1. Panicles contracted to often moderately open; glumes often with a short awn or mucro; body of lemma gradually tapering, without an evident awn column (lacking a discernable neck). ..... **Aristida purpurea** var. **parishii**
1. Panicles mostly contracted; glumes not awn-tipped; upper part of awn column often twisted, the neck (narrowed part of awn column) usually evident, often 1–2 mm long.

2. All or most panicle branches straight (lower branches sometimes lax); pedicels straight, appressed to ascending; awns 15–30 mm long..... **Aristida purpurea** var. **nealleyi**
2. All or most of the panicle branches and pedicels drooping to sinuous distally; awns (29) 35–42 mm long..... **Aristida purpurea** var. **purpurea**

Figure 5. *Aristida purpurea*. Var. *purpurea*. (A) plant and spikelet, (B) Hwy 85 near north boundary of Organ Pipe, 30 Jan 2014; (C) Hwy 86 near Quijotoa, Pima Co., 21 Sep 2004. Var. *nealleyi*. (D & E) Valley of the Ajo, drainage near Hwy 85 near mile marker 66, 28 Dec 2013.

Aristida purpurea var. **nealleyi** (Vasey) Allred
[*A. glauca* (Nees) Walpers]
Nealley three-awn, *tres barbas*. Figure 5D & E.

Perennials mostly 30–60 cm tall. Panicles mostly contracted (at first glance sometimes appearing unbranched, or exceptionally well-watered plants may reach 70 cm and the panicles not strongly contracted). Upper glume (8.5) 10–14.5 mm long, usually at least 1/3 longer than the lower glume. Lemmas 8–13.5 mm long. Awns nearly equal, 1.5–3 cm long, awn column often twisted (but not always conspicuously so), 1–2+ mm long, lighter in color than the lemma body and slightly narrowed to form the neck, drought-stressed plants tend to have a shorter columns.

One of the most common perennial grasses in the region; widespread including bajadas, hills and mountains often to their summits, valley plains often along small drainageways, and common along Highway 85; not on dunes. The history of the species or variety in the flora area extends to 11,250 years.

Var. *nealleyi* is the most wide-ranging taxon in the *A. purpurea* complex as well as in the flora area; this variety ranges from Puebla, Mexico, to southwestern USA. Some of the Organ Pipe plants might be identified as var. *purpurea*, but such specimens may be difficult to distinguish. "Although var. *nealleyi* is more distinct than the other varieties, having tufts of foliage exceeded by narrow, straw-colored panicles, it grades into var. *purpurea* (Allred 2003: 333).

OP: Bates Well, *Nichol 26 Apr 1939*. 0.7 mi N of Visitor Center on Hwy 85, 8 Sep 1984, *Van Devender 84-446*. Between Quitobaquito and Aguajita, 23 Feb 1990, *Felger 90-49*. 1 mi W of Hwy 85 near Armenta Rd, *Rutman 16 Aug 2001* (ORPI). Trail above Bull Pasture, 4090 ft, 10 Apr 2005, *Felger 05-290*.

CP: 6 mi E of Papago Wells, in wash, 11 ft, 28 Feb 1976, *McLaughlin 1044, Fugate, & McManus* (SNM). 10.5 km W of Tule Well along Camino del Diablo, 15 Mar 1983, *Reeder 7591*. Cabeza Prieta Tanks, 15 Jun 1992, *Felger 92-606*. Packrat Hill, 12 Jun 1992, *Felger 92-540*. Childs Mt, 2845 ft, 18 Aug 1992, *Felger* (observation). Sierra Pinta, summit, *Cain 15 Nov 2003*.

TA: Tinajas Altas. *Vorhies 16 Apr 1924;* 17 Apr 1948, *Kurtz 1165*. Butler Mts, *Van Devender 27 Mar 1983*. †Butler Mts, 6490 ybp (Van Devender et al. 1990: 342). †*A.* cf. *purpurea*, Butler Mts, 6490 to 11,250 ybp (3 samples, Van Devender et al. 1990: 342). †Tinajas Altas Mts, 4010 & 9700 ybp (Van Devender et al. 1990: 341).

Aristida purpurea var. **parishii** (Hitchcock) Allred
[*A. parishii* Hitchcock]
Parish three-awn

Perennials often 40–70 cm tall. Young inflorescences and spikelets dark purple-brown during winter and spring. Panicles contracted to moderately open. Glumes mostly (or at least some on each panicle) equal or subequal, the upper glume 11–13.5 mm long. Lemmas 9–13 mm long, tapering to the awn base, sometimes narrowed into a neck and slightly twisted; awns equal or nearly so, 16–27 mm long.

Localized, often as small populations and apparently not widespread in the flora area. Generally in sandy to gravelly or rocky soils along the margins of washes. Vicinity of Quitobaquito and the western margin of Organ Pipe and the eastern portion of Cabeza Prieta. Often growing near but not intermixed with *A. purpurea*. Although growing within 100 m of the Mexico border, var. *parishii* is not known for Sonora.

Variety *parishii* can be distinguished from *var. nealleyi* by its more robust habit and often moderately spreading panicle branches, subequal glumes often with a short mucro or awn, somewhat larger spikelets, and shorter awn column—without an evident and twisted neck. Allred (2003) reports that var. *parishii* flowers March–May in response to cool-season rains.

Southern California, Baja California, southern Nevada, and Arizona.

OP: Puerto Blanco Drive, 22 Oct 1964, *Ranzoni 368* (ORPI). Aguajita Wash, 3 Mar 1992, *Felger 92-102*.

CP: Agua Dulce Mts, wash, 305 m, $2n = 66$, 5 Mar 1977, *Reeder 6830*. Papago Well, 31 Jan 1992, *Felger 92-10*. 3.4 mi N of Tule Tank, 2 Feb 1992, *Felger 92-70*. Daniels Arroyo at Charlie Bell Rd, 25 Feb 1993, *Felger 93-73*.

Aristida purpurea var. **purpurea**
Purple three-awn. Figure 5A-C.

Plants to 50 cm tall. All or most of the panicle branches and pedicels drooping and often sinuous distally; awns (29) 35–42 mm long (the longer ones in a spikelet). Perhaps the few records for this variety in the flora area are robust specimens of var. *nealleyi*.

Var. *purpurea* is geographically wide-ranging but generally a non-desert taxon. There are relatively few specimens identified as this variety from the Sonoran Desert and these mostly at the margins of the desert. Some well-watered plants within the usual range of var. *nealleyi* have been identified as var. *purpurea*. Are they genetically different? Allred (2003: 333) points out that "var. *purpurea* is admittedly, a broadly defined taxon." This variety ranges from Canada to Mexico and Cuba.

OP: Valley of the Ajo, Kuakatch Wash, 450 m, fine sandy loam, uncommon, *Rutman 5 Oct 1995* (ORPI, det. J.R. Reeder 1996). Drainage N of Bates Mts and E of Bates Well Road, 32.18751° N, 112.90445° W, perennial grass on sandy loam flat, in an area where water settles and a relatively high density of perennials and annuals occur, including *Hilaria rigida*, *Prosopis velutina* and *Ambrosia deltoidea*, surrounding area relatively flat and dominated by *Larrea*, 7 Oct 2006, *Rutman 20061007-2*.

Aristida ternipes Cavanilles
Coarse, tufted perennials 0.5–1 m tall, also flowering in the first season. Roots tough and wiry. Ligules glabrous or with a sparse tuft of loose hairs. Leaf blades inrolled in drought to flat when well watered, the upper surface glabrous or with short, somewhat rough hairs. Panicles openly branched, the branches spreading to approximately 90°. Glumes subequal (spikelets at first often showing only one glume, the lower glume develops with a little more age). Awns 1 or 3 in number, 11–20 mm long (when 3 awns present, one usually longer than the others). Awn column not twisted (or only slightly so), short (1 mm or less), with no discernable neck.

There are two varieties and they have not been found growing intermixed in the flora area or across much of the Sonoran Desert. There places, however, where they do occur intermixed, such as in Catalina State Park on the west side of the Catalina Mountains above Tucson.

1. Spikelets 3-awned..... **Aristida ternipes** var. **gentilis**
1. Spikelets 1-awned..... **Aristida ternipes** var. **ternipes**

Aristida ternipes var. **gentilis** (Henrard) Allred
[*A. gentilis* Henrard. *A. hamulosa* Henrard. *A. ternipes* var. *hamulosa* (Henrard) Trent]
Poverty three-awn; *zacate araña de tres barbas*. Figure 6A.

Upper glume 12–14.5 mm long; lemmas 10–12 mm long. Awns 3, well developed but often unequal in length, the longer awn 12–20 mm long.

Common in the Ajo Mountains and scattered elsewhere in Organ Pipe. Apparently rare in Cabeza Prieta and occasional along roadsides in nearby regions.

Western Texas to southern California and southward to Guatemala.

OP: Bull Pasture, *Wirt 12 Nov 1989* (ORPI). 0.2 mi E on Bates Well Rd from intersection with Pozo Nuevo Rd, *Rutman 23 Aug 2001* (ORPI). N extension of Puerto Blanco Mts, N of Puerto Blanco Drive, 14 Mar 2003, *Rutman 2003-306* (ORPI).
CP: Just N of Jose Juan Tank, gravelly soil, several dozen plants, 14 Sep 1992, *Felger 92-710*.

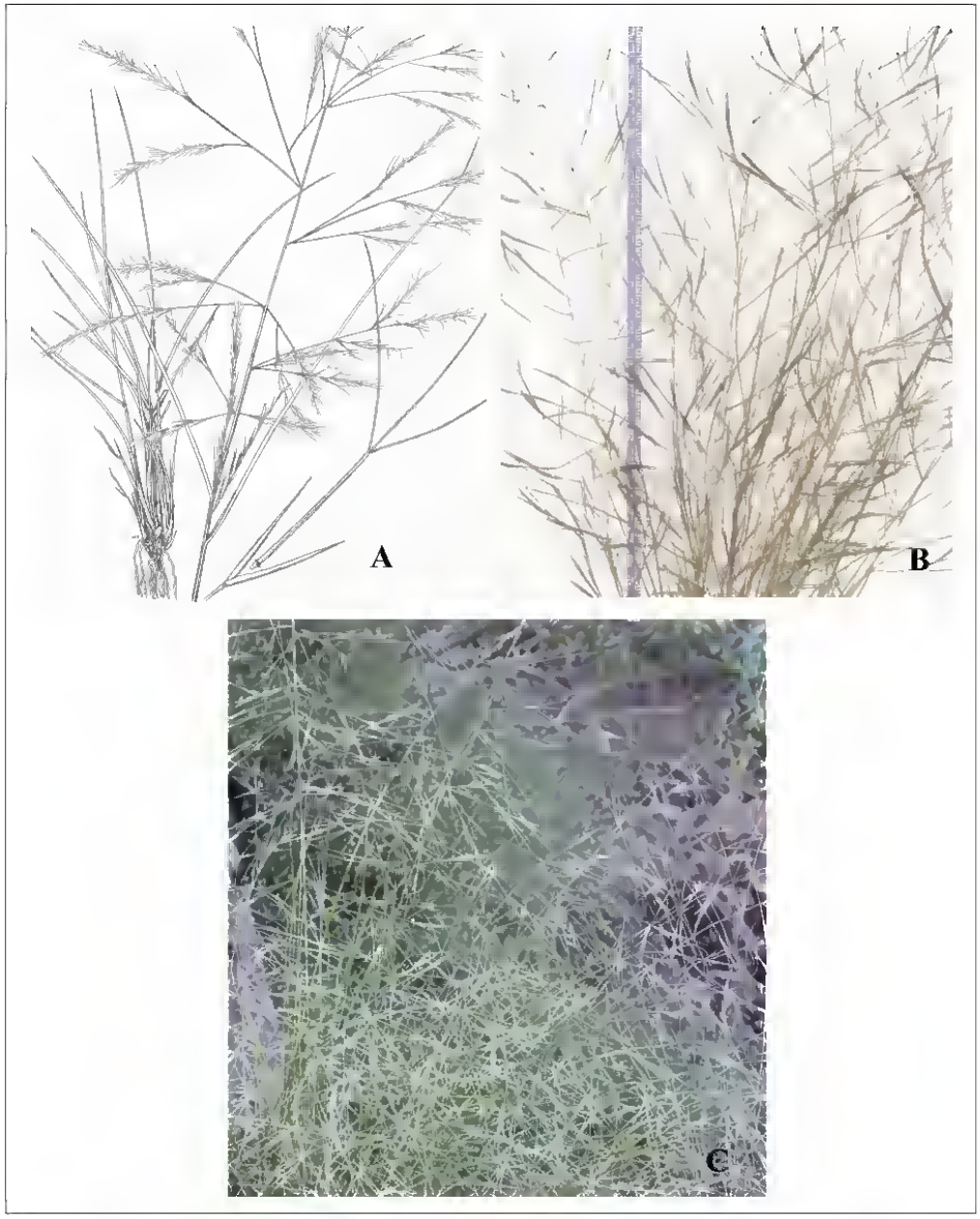

Figure 6 *Aristida ternipes* (A) Var. *gentilis* plant, panicle, and spikelet with floret separated from the glumes, Var *ternipes* (B) Chuckwalla Hills, Organ Pipe, 5 Oct 2013, (C) Bull Pasture, Ajo Mts, 25 Sep 2013

Aristida ternipes var **ternipes**
Spider grass, *zacate araña* Figure 6B-C

Upper glume 10–15 mm long, lemmas 13–19 mm long, with one well-developed awn, straight or moderately curved, 11–14 mm long. The lateral awns fail to develop or are present but greatly reduced.

Canyons and slopes, fairly common at scattered mountain localities across Cabeza Prieta and much of Organ Pipe including the Ajo Mountains.

Arizona to Texas and South America, and the West Indies.

OP Alamo Canyon, *Nichol 4 May 1939*. Ajo Mt Drive, 2000 ft, 5 Nov 1977, *Bowers 917*. Diablo Mts, grassy slopes, 12 Sep 2013, *Rutman 20130912-2*.
CP Agua Dulce Spring, 13 Jun 1992, *Felger 92-579b*. Eagle Tank, 13 Jun 1992, *Felger* (observation).

Avena fatua Linnaeus. Figure 7.
Wild oats; *avena silvestre, avena cimarróna, avena loca*; 'agspĭ mudat-kam, ko:ksam

Winter-spring ephemerals, often 0.5+ m tall (occasionally to about 1 m). Panicles open and sparse, the branches drooping. Spikelets relatively large, on long, slender, and often curled pedicels, mostly with 2 or 3 florets, breaking apart above the glumes and between the florets. Glumes 2–3 cm long, thin and longer than the florets. Lemma often 1.5–2 cm long with red-brown hairs and a stout awn 3.5–4.5 cm long, strongly twisted below and bent at the middle.

Widely scattered in Organ Pipe where it has become locally more common since about 2000.

Native of Eurasia; widely naturalized and weedy including western North America. Common along roadsides north and east from Ajo, AZ. Cultivated oats are *A. sativa*.

OP Bull Pasture, 2 May 1978, *Bowers 1275*. Eagle Pass, base of hills, Hwy 85, N end Diablo Mts, *Rutman 14 Apr 1998*. Estes Canyon, 18 Mar 2005, and 25 Apr 2013, *Rutman*, photos.

Figure 7. *Avena fatua*. (A) Plant, leaf, panicle, and spikelet; (B) Javelina Mts, Maricopa Co., 5 Mar 2005.

Bothriochloa barbinodis (Lagasca) Herter
[*Andropogon barbinodis* Lagasca]
Cane bluestem; *zacate popotillo.* Figure 8.

Figure 8. *Bothriochloa barbinodis.* (A) Bull Pasture, 25 Sep 2013; (B) panicles, east of Why, Pima Co., 15 Sep 2013.

Robust tufted perennials often 0.75–1 m tall; growing and reproductive during warm weather. Usually villous with dense tufts of long, white hairs at nodes, ligules, and on inflorescences. Leaves drying reddish brown, at least the bases semi-persistent; leaf blades flat. Fresh, crushed pieces of the plant, especially the inflorescences, often have a mild blueberry-like fragrance. Inflorescences of terminal panicles, the branches simple rames or sparingly rebranched. Panicles 5–11 cm long, white and cottony, with numerous branches clustered at the top of tall, nearly naked culms. Spikelets andropogonoid, the rames (individual stalks of the spikelet pairs or triplets, the rachis joints, and pedicels) with a central groove or membranaceous area appearing as a thin, translucent or "naked" area; rachis joints and pedicels with hairs reaching 6–8 mm long. Glumes of both spikelets large and firm (indurate). Glumes of the sessile (fertile) spikelets about equal in size, 5–5.5 mm long, but

differently shaped: lower glume broad, green, and flat to concave on the back; upper glume markedly humpbacked or V-shaped with a blunt keel (ridge). Fertile lemma bearing a stout, twisted, bent awn 14–22 mm long. Sterile (pedicelled) spikelet reduced to a deciduous linear rudiment 3.5–4 (5) mm long.

Abundant at the high elevations in the Ajo Mountains and much less common at lower elevations. West of the Puerto Blanco Mountains in Organ Pipe, it is found in places of higher than usual soil moisture such as near waterholes and seeps along canyon bottoms. In Cabeza Prieta locally in the vicinity of Cabeza Prieta and Tule Tanks and in the Tinajas Altas Region it has been observed in the mountains above the tanks. This grass occurred in the Puerto Blanco Mountains about 5200 years ago, and this or a similar grass grew in the Ajo Mountains about 8000 to 9500 years ago.

Scattered populations occur in the Sonoran Desert, but the species is much more common and widespread at elevations above the desert in Arizona, the eastern part of Sonora, and mountains in Baja California Sur.

Southwestern USA to South America.

OP: Alamo Canyon, *Nichol 4 May 1939*. Ajo Mt Drive 6 7 mi NE of Visitor Center, 5 Nov 1977, *Bowers 911*. Entrance to Arch Canyon, 2 Dec 1990, *Felger 90-522*. Diablo Mts, wash, along Ajo Mt Drive, 12 Sep 2013, *Rutman 20130912-10*. †Puerto Blanco Mts, 5240 ybp (Van Devender et al. 1990: 339). †*B.* cf. *barbinodis*, Alamo Canyon, florets, 8130 & 9570 ybp (Van Devender et al. 1990: 339).

CP: Tule Tanks, 4 Dec 1935, *Goodding 127*. Cabeza Prieta Tanks, 15 Jun 1992, *Felger 92-605*.

TA: Tinajas Altas, canyon bottom just above uppermost tinaja, 19 Mar 1998, *Felger* (observation)

Bouteloua – Grama grass; *navajita*

Diverse ephemerals and perennials. Culms and inflorescence axes slender. Leaves mostly basal; ligules membranous, ciliolate, or a fringe of hairs. Inflorescences panicles with 2–many spicate, unilateral branches arranged in a racemose pattern or sometimes 1 per inflorescence. Inflorescence branches persistent or falling entire; spikelets relatively small, in 2 rows arranged at the margins along one side of a flattened rachis. These spicate, unilateral branches are an easily recognized feature (even *B. aristidoides* with its small branches has a flat-topped rachis). Spikelets variously awned, with 1 bisexual or unisexual floret below, and 1–3 staminate or sterile and usually smaller and different-looking florets (rudiments) above. Glumes unequal. Lemma of fertile floret with 3 veins, awnless or the veins often extending into short awns, and the palea with 2 veins and also awnless or the veins often extending into short awns.

Two summer ephemerals, *B. aristidoides* and *B. barbata* var. *barbata*, are widespread and often abundant across the Sonoran Desert. Other bouteloua are much less widespread in the desert; the perennial species are much more common and widespread in regions above or beyond the desert. Grama grasses are esteemed for forage.

1. Ephemerals, usually growing with summer rains; roots often weakly developed; lower leaves few, internodes between them readily visible.

    2. Panicle branches (spicate branches) needle-arrow shaped, with 1–4 slender spikelets closely appressed to the branch axis (not spreading) ..... **Bouteloua aristidoides**
    2. Panicle branches pectinate (comb-like), often with 20–50 spikelets, these crowded in a double row and spreading perpendicular to the spike axis..... **Bouteloua barbata** var. **barbata**

1. Perennials with hard, knotty bases; roots well developed; basal (lower) leaves densely clustered, internodes between lower leaves usually very short and often not readily visible.

3. Panicle branches pectinate, more or less persistent.

4. Spikelet awns (on lemmas) to 3 mm long; lemmas pubescent below with white hairs..... **Bouteloua barbata** var. **rothrockii**
4. Spikelets awns 5 mm long or more; lemmas glabrous or nearly so..... **Bouteloua trifida**

3. Panicle branches not pectinate, readily deciduous as a whole.

5. Panicle usually with more than (18) 20 branches..... **Bouteloua curtipendula**
5. Panicle with fewer than 15 branches..... **Bouteloua repens**

Bouteloua aristidoides (Kunth) Griesebach
[*B. aristidoides* var. *arizonica* M.E. Jones]
Six-weeks needle grama; *aceitilla, navajita aguja.* Figure 9.

Summer-fall ephemerals usually with rather weakly developed roots. (Sometimes a few plants overwinter, resume growth, and flower in spring, or rarely germinate and grow in the spring but these plants are stunted.) Highly variable in size. Culms and panicle axes delicate, slender, erect to spreading-ascending, 10–30 (70) cm long. Ligule a fringe of hairs. Panicle branches 8–22 mm long, 11–16 (24) per stem, slender and needle-arrow-like, and readily falling at maturity together with their several spikelets, or spikelets falling separately. (These can be bothersome, sticking in socks and shoes. People are probably supplanting animals as dispersal agents.) Spikelets (1 or 2) 3 (4–10) per branch, appressed to the rachis; rachis flattened, ciliate, curving out from the attachment of the terminal spikelet, which it about equals or exceeds in length. Lowermost spikelet sub-sessile, with 1 floret, awnless, and without a rudiment. Upper spikelets short-pedicelled, bearing a sessile, awnless, fertile floret and a sterile floret with a short stipe and 3 conspicuous *Aristida*-like awns 2.5–6 mm long. Grain golden brown, oblong, flattened, with a prominent dorsal groove.

Seasonally common and widespread in many habitats across the region, reaching peak abundance on sandy loams in valley bottoms or lower bajadas. The common name describes the ability of plants to reach reproductive size in a short period of time. Generally more numerous than *Bouteloua barbata* var. *barbata*, the only other ephemeral grama grass in the region. *Bouteloua aristidoides* has been widespread across the region for at least 21,900 years.

This is one of the most abundant hot-weather ephemerals in the Sonoran Desert. The great success of this grass in the desert seems to be partly due to plasticity in size and number of structures and to rapid growth and reproduction. As soon as the grain ripens and the plants dry, *Pogonomyrmex* harvester ants stream out along their paths and carry home the whole, disarticulated spikelets. At their nest they remove the grain and pile the chaff in crater-like mounds around the entrance to their subterranean colonies.

Southwestern USA to Argentina. *Bouteloua aristidoides* growing during highly favorable conditions may become relatively large and vigorous; such plants have been called var. *arizonica* M.E. Jones.

OP Alamo Canyon, 10 Apr 1952, *Fouts 447* Armenta Well, *Warren 16 Nov 1974.* Aguajita, 13 Sep 1986, *Felger 86-280.* 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-16.* N end Bates Mts, 11 Sep 2013, *Rutman 20130911-4* †Alamo Canyon, florets, 14,500 ybp

Figure 9. *Bouteloua aristidoides*. (A & D) Alamo Canyon, Ajo Mts, 15 Sep 2013. Valley of the Ajo, W of Hwy 85 at mile marker 60: (B) 16 Aug 2006; (C) Ants collecting spikelets, 7 Oct 2008.

†Montezuma's Head, spikelets, florets, and fragments, 13,500 to 21,840 ybp (3 samples) †Puerto Blanco Mts, 980 to 10,540 ybp (8 samples, Van Devender et al. 1990: 339) E of Armenta Ranch, *Rutman 30 Sep 2006*.

CP: Bates Well Rd at Organ Pipe boundary, 14 Sep 1992, *Felger 92-682* (CAB, UC). Childs Mountain, 2845 ft, 18 Aug 1992, *Felger 92-643*. Daniels Arroyo at Charlie Bell Rd, 18 Aug 1992, *Felger 92-667*. Growler Valley, 25 Sep 2013, *Rutman 20130926-2*.

TA: Tinajas Altas, above the tinajas, 19 Mar 1998, *Felger* (observation). Coyote Water, 25 Oct 2004, *Felger 04-31*. †Butler Mts, 610 to 11,250 ybp (6 samples, Van Devender et al. 1990: 342) †Tinajas Altas Mts, 4010 & 8700 ybp (Van Devender et al. 1990: 341).

Bouteloua barbata Lagasca

Panicle branches pectinate (comb-like), nearly straight to arched. Ligules membranous–ciliolate. The two varieties occupy different ecological and geographic ranges.

1. Ephemerals, the root system often weakly developed. ..... **Bouteloua barbata** var. **barbata**
1. Perennials with a hard, knotty base, the root system well developed. ..... **Bouteloua barbata** var. **rothrockii**

Bouteloua barbata var. **barbata**

Six-weeks grama; *navajita, zacate liebrero*; s-cuk mudadt-kam. Figure 10 A–C.

Summer-fall ephemerals (rarely growing with spring rains and then stunted). Roots weakly developed. Usually branched from near the base, the culms and panicles 5–50 (80+) cm long, geniculate-spreading (abruptly bent upward from near the base of the plant) to erect and straight, or sometimes prostrate. Panicles with (1) 4–12 branches, (6) 10–25 (30) mm long, pectinate, nearly straight to arched. Spikelets often 20–54 per branch, 2.2–3.5 (4.5) mm long (including awns), crowded, more or less in 2 rows and at right angles to axis of spike. First (basal) floret in the rudiment with 3 short awns on a column. Upper florets of the rudiment greatly reduced and consisting of tiny petal-like structures on top of awn bases of the first (lower) sterile floret. Anthers cream colored, pale yellow, orange, or red.

Widespread including sand flats, valley floors, and bajadas to hills and mountains. On sandy loams of the valley floor and lower bajadas in Organ Pipe, *Bouteloua barbata* along with *B. aristidoides* can form carpets of ephemeral grasses. Together with *B. aristidoides* it is seasonally abundant in many habitats across the region as well as through most of the Sonoran Desert.

Southwestern USA to southern Mexico (Oaxaca) and disjunct in Argentina.

OP: Ajo Mts, *Begeman 1968* (ORPI). Aguajita, 13 Sep 1986, *Felger 86-279*. Armenta Ranch, *Wirt 8 Sep 1990* (ORPI). 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-7*. Growler Valley, *Rutman 23 Aug 2001* (ORPI).

CP: Bates Well Rd at Organ Pipe boundary, 14 Sep 1992, *Felger 92-683*. Daniels Arroyo at Charlie Bell Rd, 18 Aug 1992, *Felger 92-668*. Jose Juan Represo, 12 Jun 1992, *Felger 92-561*. Las Playas, 28 Nov 2001, *Felger 01-578*. San Cristobol Wash, 26 Sep 2013, *Rutman 20130926-12*.

TA: Coyote Water, 25 Oct 2004, *Felger 04-32*. Tinajas Altas, 25 Oct 2004, *Felger 04-70*.

Bouteloua barbata var. **rothrockii** (Vasey) Gould

[*B. rothrockii* Vasey]

Rothrock grama; *zacate liebrero*. Figure 10 D & E.

Tufted perennials with a hard, knotty base at or below the soil surface and well-developed roots. Stems most often straight and erect. Panicles with 4–8 (10) branches. Stigmas blue; anthers red or yellow. Growing and reproductive during the warmer months, especially following summer-fall rains.

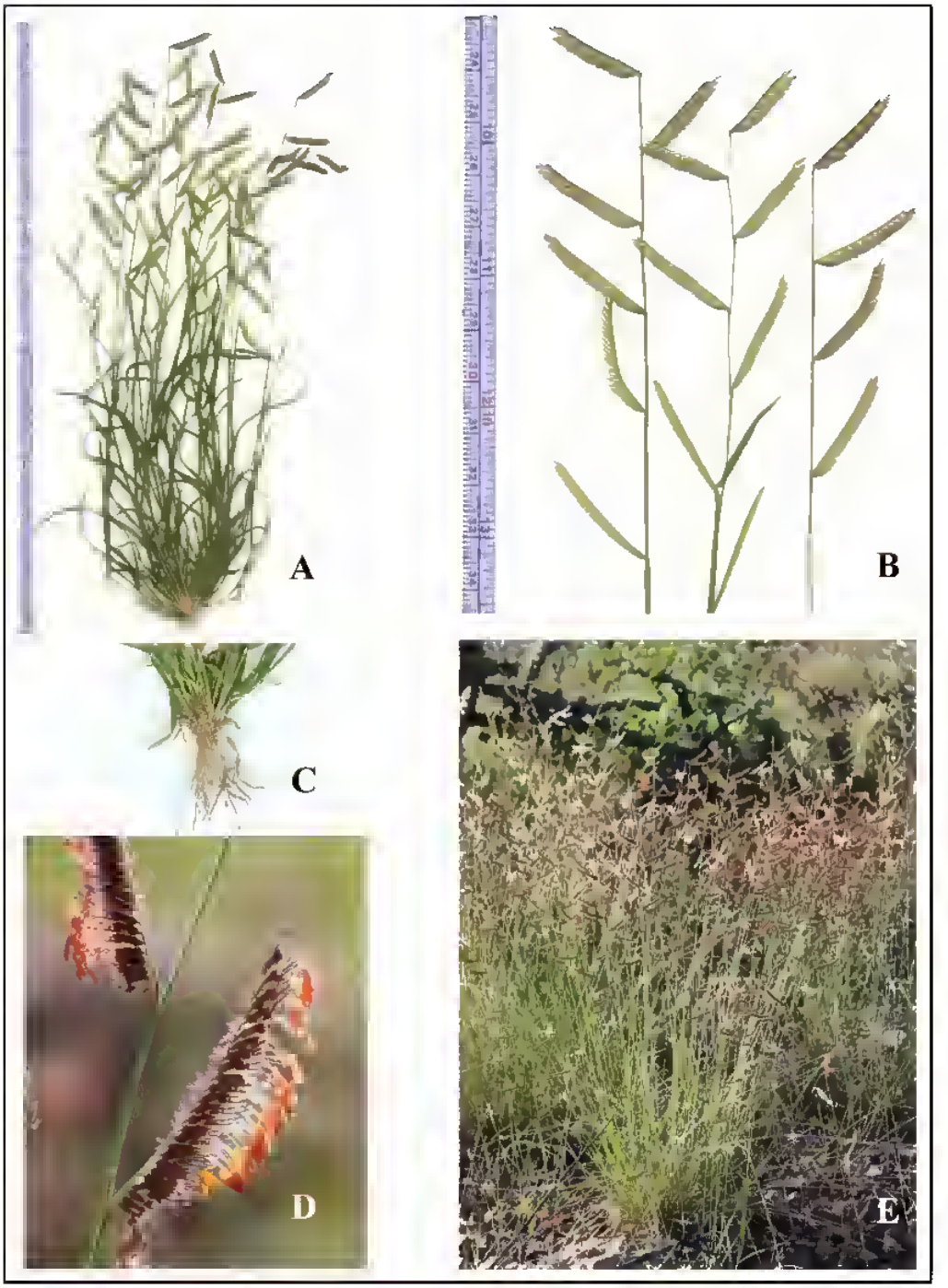

Figure 10 *Bouteloua barbata*. Var. *barbata* (A & B) Hwy 85 near N boundary of Organ Pipe, 15 Sep 2013. (C) Valley of the Ajo, W of Hwy 85 at mile marker 60, 10 Sep 2006. Var. *rothrockii* (D & E) Diablo Mts, 14 Sep 2013.

Common at mid- and upper elevations in the Ajo Mountains, and locally common in the Bates and Diablo Mountains and probably elsewhere in larger mountains in Organ Pipe.

Western and southern Arizona, generally above the desert. Southern California, Arizona, southwestern and central New Mexico, and northwestern and north-central Mexico.

OP: Ajo Mt Drive, 6.7 mi by road NE of Visitor Center, 2000 ft, 5 Nov 1977, *Bowers 913*. Bull Pasture Trail, rocky slopes, 2500 ft, 9 May 1979, *Bowers 1708*. Rocky slope NW of Kino Peak, 1782 ft, 20 Mar 2005, *Rutman 2005-0320-46* (ORPI).

†Bouteloua barbata var. **barbata** and/or var. **rothrockii**

One or more likely both of these grama grasses are well represented in the fossil record across the flora region for at least 21,900 years. The two taxa are distinguished by growth form (ephemeral verses perennial) and cannot be distinguished by the fossils, which are fragments of reproductive parts.

OP: †Alamo Canyon, 1150 ybp. Montezuma's Head, 20,490 ybp. Puerto Blanco Mts, 130 to 9720 ybp (9 samples, Van Devender et al. 1990: 339).
TA: †Tinajas Altas Mts, 5080 & 8700 ybp (Van Devender et al. 1990: 341).

Bouteloua curtipendula (Michaux) Torrey
Sideoats grama; *banderilla*; da:pk vasai. Figure 11.

Tufted perennials often 40–70 cm tall; culms slender, often with 4 or 5 nodes above the base of the plant. Panicles bearing (18) 25–80 branches, these often 1–2.5 cm long, slender, evenly spaced, drooping, and deciduous at maturity; branches each with 2–7 spikelets; upper glumes often 6–8 mm long. Anthers red-orange. Growing and reproductive during the warmer months, especially following summer-fall rains.

Ajo and Puerto Blanco Mountains, most common at higher elevations. These plants align with the widespread var. *caespitosa* Gould & Kapadia, but the varieties seem poorly defined (Siqueiros-Delagado et al. 2013). *Bouteloua curtipendula* has been in the Ajo Mountains for at least 20,500 years.

Widespread in Arizona, generally at the upper elevation limits and above the desert. Canada to South America.

OP: Alamo Canyon, *Nichol 4 May 1939*. Arch Canyon, *Rutman 8 Nov 1995* (ORPI). Ridge NNE of Pinkley Peak, 31 Oct 2003, *Rutman 2003-1031-22* (ORPI). Diablo Mts, wash, along Ajo Mt Drive, 12 Sep 2013, *Rutman 20130912-7*. †Alamo Canyon, florets, 1150 to 9570 ybp (4 samples). †Montezuma's Head, florets, 13,500 & 20,490 ybp.

Bouteloua repens (Kunth) Scribner & Merrill
[*B. filiformis* (E. Fournier) Griffiths]
Slender grama; *navajita delgada*. Figure 12.

Perennials mostly 15–50 cm tall, forming dense, knotty bases, not rhizomatous. Roots wiry and well developed. Leaves mostly basal. Apparently capable of flowering at any time of year but especially with warm weather, and also flowering in the first year but then the spikelets often not maturing. Panicles mostly with (2) 4–12 branches, these 10–20 mm long, relatively broad, deciduous at maturity, and bearing spikelets 9–13 mm long. Pedicels, rachises, and glume veins with short, coarse hairs. Anthers yellow or orange.

Widespread in the Ajo and Puerto Blanco Mountains and locally elsewhere in Arizona Upland portions of Organ Pipe; often on shallow rocky soils or in crevices on bedrock. Its history in

the Ajo Mountains extends to more than a millennium and it was in the western edge of the flora region at least 8200 years ago.

Western and southern half of Arizona to Texas and through Mexico to Central America, the Caribbean and northern South America

OP: Alamo Canyon, 2500 ft, 3 Dec 1977, *Bowers 980*. Diablo Canyon, *Van Devender 20 Jan 1984* (ORPI) Ajo Mt Drive 2.3 mi E of Visitor Center, 1750 ft, large wash, 9 May 1985, *Van Devender 85-113*. Diablo Mts, 2480 ft, grassy slopes, 12 Sep 2013, *Rutman 20130912-4*. †Alamo Canyon, florets, 1150 ybp.
TA: †Butler Mts, 8160 ybp (Van Devender et al. 1990: 342)

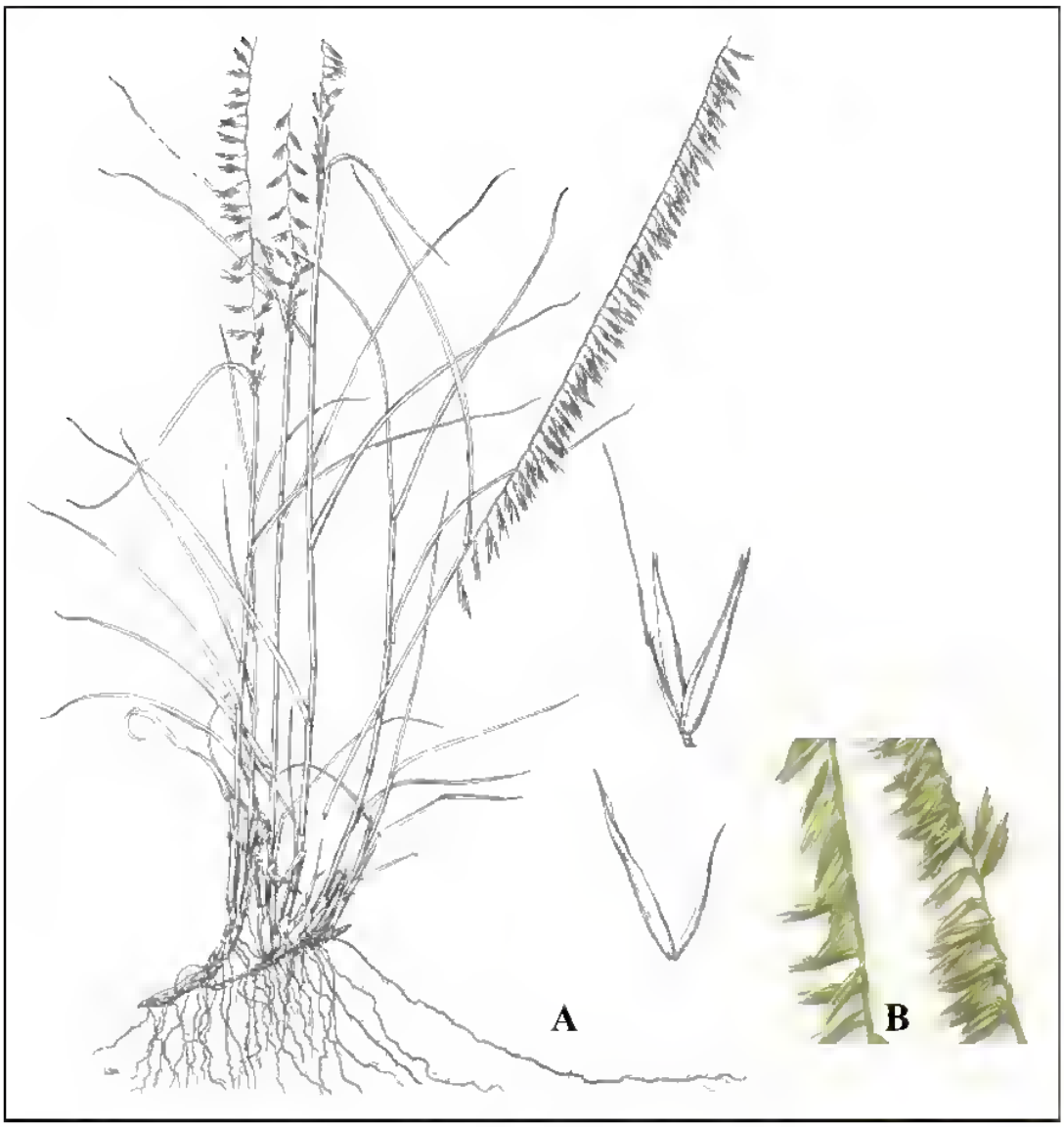

Figure 11. *Bouteloua curtipendula*. (A) Plant and spikelet, (B) portion of panicle with spikelets, Alamo Canyon, Ajo Mts, 15 Sept 2013.

Figure 12 *Bouteloua repens* Diablo Mts (A) 22 Sep 2013, (B) 14 Sept 2013

Bouteloua trifida Thurber
Red grama, *navajita china* Figure 13

Small tufted perennials, (5) 12–30 (40) cm tall, with hard knotty bases and sometimes with short rhizomes, occasionally forming "fairy ring" colonies. Leaves mostly basal. Panicles with 2–6 branches, pectinate, bristly, purplish, and persistent, often reddish when young.

This small grama grass is found at widely scattered localities across the northern part of the Sonoran Desert. It is much more prevalent above the desert. A single fossil record establishes it in Organ Pipe Cactus National Monument about 1000 years ago.

Canyons, arroyos, rocky slopes, and mesas, widely scattered and often local populations in some of the mountains in Cabeza Prieta and Organ Pipe. Often growing from crevices in bedrock. It is probably more common than collections indicate.

This species is unusual among grama grasses in that it has adapted to a winter rainfall regime, at least in the western part of the Sonoran Desert Region, where it seems to grow and flower at almost any time of year.

Southern Utah to southern California and Texas, and drier regions of northern and central Mexico including Baja California, Chihuahua, Coahuila, Nuevo León, San Luis Potosí, northern Sonora, and Tamaulipas.

OP: Gunsight Hills, on granite, *Rutman 4 Apr 1998* (ORPI). Granite foothills, NW side Puerto Blanco Mts, *Rutman 7 Apr 1998* (ORPI). NW of Kino Peak, Bates Mts, 20 Mar 2005, *Rutman 2005-0320-46*. Puerto Blanco Mts, Red Tanks Wash, 21 Sep 2013, *Rutman 20130921-1*. †Puerto Blanco Mts, 980 ybp (Van Devender et al. 1990: 339).

CP: 0.5 mi above Gray Tank, T2S, R19W, S35, dry wash, 8 Dec 1985, *Russo 251*. Eagle Tank, 13 Jun 1992, *Felger 92-587*. Little Tule Well, 18 Aug 1992, *Felger 92-648*. Childs Mt, 2240 ft, 9 Apr 1993, *Felger 93-304* (CAB).

Figure 13. *Bouteloua trifida*. (A) Plant and spikelet with glumes and florets separated; (B) spicate branches on portions of two panicles, Gunsight Hills near Kuakatch Village, 10 Sept 2013; (C) Estes Canyon, Ajo Mts, 2 Apr 2010.

Bromus – Chess, brome

The Sonoran Desert populations are winter-spring ephemerals; no *Bromus* survives the Sonoran Desert summer. In wetter regions many brome grasses are perennials. Leaf-sheath margins closed to near the top of the sheath. Ligules membranaceous; auricles none (those in the flora area). Panicles open or compact; spikelets relatively large, with several florets, laterally compressed or turgid and only slightly compressed, breaking apart above glumes and between florets; the florets often cleistogamous. Glumes persistent, usually unequal, lanceolate, shorter than the florets (excluding awns). Florets (lemmas) often progressively smaller above but similar in shape to the lower ones. Lemmas 1-awned from a notch between the bilobed tip or awnless. Ovary capped by a hairy bilobed appendage bearing sub-terminal stigmas.

1. Spikelets conspicuously flattened (laterally compressed), upper glumes 5- or 7-veined, lemmas strongly keeled, V-shaped in cross section ..... **Bromus arizonicus**
1. Spikelets rounded in cross section, upper glumes 3- or 5-veined; lemmas not strongly keeled, U-shaped in cross section

2. Panicles compact and dense, the branches very short and spikelets mostly erect ..... **Bromus rubens**
2. Panicle open, the branches and pedicels rather long and conspicuously curving-drooping, spikelets mostly not erect ..... **Bromus tectorum**

Bromus arizonicus (Shear) Stebbins
[*B. carinatus* Hooker & Walker var. *arizonicus* Shear]
Arizona brome. Figure 14.

Figure 14. *Bromus arizonicus*. (A) Plant and spikelet; (B) panicle, Alamo Well, Alamo Canyon, Ajo Mts, 18 Mar 2005.

Slender grasses (20) 50–120 cm tall. Spikelets conspicuously laterally compressed when young, but less so as the grain matures. Lower glumes 7–12 mm long, with 3–5 veins; upper glumes 8–18 mm long, with 5–7 veins. Lemmas 11–15 mm long, strongly keeled, V-shaped in cross section, with 7–11 veins, and a stout awn often 4–11 mm long.

Abundant along drainageways during favorable years, especially El Niño years. Organ Pipe and the eastern part of Cabeza Prieta. This brome can form near pure stands in localized areas of large washes, e.g., Alamo, Cherioni, Kuakatch, and San Cristobal Washes.

California to New Mexico, Nevada, Baja California Norte, and northernmost Sonora.

Bromus arizonicus is part of the *B. carinatus* complex (e.g., Pavlick et al. 2007; Saarela & Peterson 2012; Saarela et al. 2014). *Bromus carinatus* is a short-lived perennial, native from Alaska to Central America and apparently is not native within the Sonoran Desert. Sonoran Desert *B. arizonicus* specimens do not seem separable from *B. carinatus* when a suite of specimens are examined. Plant sizes, relative glume lengths, spikelet sizes, and sometimes even numbers of veins in spikelet parts can vary to a maddening degree, undoubtedly influenced by environmental conditions, especially soil moisture. Should the *arizonicus* taxon be recognized?

OP: 9 mi S of N entrance to the Monument, Sonoyta road, 8 Apr 1941, *McDougall 46*. Alamo Canyon, *Tinkham Apr 1942*. Bull Pasture Trail, 5 Apr 1978, *Bowers 1209*. Growler Canyon, 30 Mar 1979, *Bowers 1602*. Puerto Blanco Mts, 2 mi NW of Visitor Center, 8 Mar 1987, *Van Devender 87-7*.

CP: San Cristobal Wash, 31 Jan 1992, Felger 92-2. Daniels Arroyo on Charlie Bell Rd, 12 Jun 1992, Felger 92-541. Little Tule Well, 9 Apr 1993, Felger 93-334. Papago Well, 26 Mar 2010, Felger 10-112.

***Bromus rubens** Linnaeus
[*B. madritensis* Linnaeus subsp. *rubens* (Linnaeus) Husnot]
Red brome; *bromo rojo*. Figure 15.

Plants often 10–25+ cm tall, hairy especially on leaf sheaths and stems, the hairs often soft and retrorse (backward pointing) on leaf sheaths. Panicles densely contracted, brush-like, the branches and spikelets mostly upright, more or less sessile, and not compressed (flattened). Lower glumes 5–8 mm long, with 1 (3) veins; upper glumes 10–15 mm long, with 3–5 veins. Lemmas 10–15 mm long and hairy, with slender bifid terminal teeth (lobes) 1–3 mm long, and an awn 12–26 mm long, stiff, stout, straight or slightly curved but not bent or twisted. Sometimes germinating as early as September.

Across most of Organ Pipe, often abundant in the Ajo Mountains to the crest, but less common and localized elsewhere. Well established in Cabeza Prieta, especially in the eastern portion; washes, plains, and many mountains to peak elevations. Also in the Tinajas Altas Region but not common.

Red Brome has become abundant in southern Arizona and across the northern part of Sonora, especially since the 1970s (Bowers 1980; Felger 1990, 2000). It has been present in the Ajo Mountains at least since 1942 and in the town of Ajo since 1916. It is invasive nearly throughout the region and with favorable rains can become dense enough to carry a fire when dry.

This weedy Mediterranean grass, adventive and common through much of the western USA, was established in California by 1848 (Frenkel 1970). Red brome seeds in the Sonoran Desert soils have a relatively short life span, which has important conservation implications (Salo 2004).

OP: Alamo Canyon, 2000 ft, *Tinkham 18 Apr 1942*. Arch Canyon, 5 Apr 1978, *Bowers 1180* (ORPI). Residence area, 30 Mar 1988, *Felger 88-139*. Hocker Well, 10 Apr 1996, *Rutman* (observation). Cherioni Wash near Hwy 85, *Rutman 12 May 2003*. Trail from Bull Pasture to crestline, 10 Apr 2005, *Felger 05-247*.

CP: San Cristobal Wash at Bates Well Rd, 14 Sep 1992, *Felger 92-694*. Chico Suni temporal, NW of Bassarisc Tank, Antelope Tank, 12 & 13 Jun 1992, *Felger* (observations). Charlie Bell Road near E boundary of Refuge, 9 Apr 1993, *Felger 93-324*. Jose Juan Tank, 26 Feb 1993, *Felger 93-102* (CAB).

TA: Camino del Diablo at Coyote Wash, 10 Jan 2002, *Felger 02-8*. Tinajas Altas, 30 Dec 2005, *Felger 05-483*.

****Bromus tectorum** Linnaeus
Downy chess, cheat grass

Panicles branched, the branchlets and pedicels slender, curved, and drooping under the weight of the relatively large spikelets. Spikelets 10–20 mm long, often reddish brown, laterally and moderately compressed. Lower glumes 4–9 mm long, with 1 vein, upper glumes 7–13 mm long, with 3 or 5 veins. Lemmas 10–12 mm long, hairy, with an awn 12–14 mm long and straight.

Known from two records and not known to be reproducing in Organ Pipe. Generally not well established in the Sonoran Desert. Fairly common in Arizona above the desert and non-desert regions of northern Baja California and especially California. Native to Europe and extensively naturalized in temperate North America and elsewhere.

OP: International fence at El Papalote, adjacent to Aguajita Spring, 9 Apr 1986, *Felger 86-133*. Visitor Center parking lot, one plant, 15 Mar 1998, *Rutman* (observation, plant removed).

Figure 15. *Bromus rubens*. (A) Plant, spikelet, and single lemma. Alamo Canyon, Ajo Mts. (B) 12 Mar 2005; (C) 7 Feb 2013.

Cenchrus – Sandbur, buffelgrass, and fountain grass
[*Pennisetum*]

Highly diverse ephemerals and perennials. Panicles spike-like, bearing spikelets enclosed in burs with fused, flattened, barbed spines (*Cenchrus* sensu stricto) or panicles more or less contracted with spikelets enclosed in fascicles of bristles (*Pennisetum*), the burs or fascicles fall with the spikelets as a unit; the spines and bristles are derived from modified branchlets. Spikelets panicoid, with 2 florets, the lower floret staminate or sterile, the upper one bisexual. See Chemisquy et al. (2010) and Columbus and Smith (2010) for uniting *Pennisetum* and *Cenchrus*.

1. Spikelets enclosed in burs, the spines united, at least below (*Cenchrus* sensu stricto).

2. Inflorescences with 1–3 burs; larger spines of bur (6) 9–15 mm long ..... **Cenchrus palmeri**
2. Inflorescences usually spike-like with 10 or more burs; larger spines of bur 3.5–6 mm long.

3. Basal bristles slender, many in a ring, the larger flattened spines of different sizes and more or less in a single whorl..... **Cenchrus echinatus**
3. Basal bristles none to several, not forming a ring, the larger flattened spines mostly of the same size and at different positions on the bur..... **Cenchrus spinifex**

1. Spikelets in fascicles with distinct or nearly distinct bristles (*Pennisetum*).

4. Panicles (1.5) 4.5–10 cm long; longer spikelet bristles 7–12 (15) mm long; basal bristles often slightly united..... **Cenchrus ciliaris**
4. Panicles 13–26 cm long; longer spikelet bristles 18–35 mm long (ignore occasional shorter-bristled spikelets at the tip of the panicle); basal bristles not united..... **Cenchrus setaceus**

***Cenchrus ciliaris** Linnaeus
[*Pennisetum ciliare* (Linnaeus) Link]
Buffelgrass; *zacate buffel*. Figure 16.

Robust perennials often 0.5–1 m tall, often with a knotty base, and often flowering in the first season; growing and flowering during the warmer months. Leaves often reddish during cool weather; leaf sheaths laterally compressed and keeled, glabrate to sparsely pilose with long slender hairs; hairs near collar usually sparse, white, and straight, reaching 5 mm with enlarged bases, the ligule membranous, ciliate; leaf blades glabrate, scabrous, or sparsely pilose, especially on lower surface, larger blades 23–34 cm × 7–10 mm, the midrib prominent. Panicles 4.5–12.5 cm long, densely flowered and contracted. Fascicles essentially sessile; bristles mostly united at the very base, flexible and somewhat sinuous, often purplish brown, unequal in length, plumose basally with spreading silky white hairs, the larger bristles 8–13.5 mm long and conspicuously flattened, the outer bristles in a loose ring around the fascicle base, much smaller, many, slender, terete, and scabrous. Spikelets 4.5–5.5 mm long, sessile or subsessile, 2 or 3 per fascicle.

Buffelgrass has been well established along Mexico Highway 2 just south of the flora area since at least the 1970s (Felger 1990, 2000) and spread into Organ Pipe where the first documented record was in 1984. It rapidly increased in abundance in Organ Pipe in the 1980s and was found in relatively small but growing populations throughout the Monument. Relatively small (less than 1 acre) but rapidly expanding colonies of buffelgrass are common throughout Organ Pipe (2010–2013) and in the eastern mountains of Cabeza Prieta on all soil types. It shows the least preference for dunes and Pleistocene-aged surfaces. Low summer rainfall probably limits its growth and expansion in the western part of the flora area and is only weakly established at the margins of the Tinajas Altas

Figure 16. *Cenchrus ciliaris*. (A) Valley of the Ajo, Organ Pipe, 6 Oct 2012 Ajo, Pima Co.; (B & C) detached spikelets and panicles, 15 Apr 2013; (D) summit of leaf sheath at collar area, 25 Mar 2013.

region at the Sonora border. It is abundant all along Mexico Hwy 2 just south of the flora area, as far west as the granitic mountains south of the Tinajas Altas Region (e.g., Felger 2000).

Native to the warmer parts of Africa, Madagascar, and India, and introduced in many hot, semi-arid regions of the world for forage and fodder. Widely planted as a forage grass in Sonora, it has become a serious invasive weed in southern Arizona and Sonora.

Since 1994 the National Park Service has conducted an aggressive, labor-intensive program of manual removal of this tenacious invasive weed in some areas of Organ Pipe with successful results, but as long as sources of infestation remain the program needs constant attention (Rutman 2010). The U.S. Fish and Wildlife Service has also conducted an eradication program on Cabeza Prieta, mostly centered on Childs Mountain.

In the 1940s the U.S. Department of Agriculture Plant Materials Center in Tucson introduced buffelgrass into the southwestern USA for soil erosion control and livestock forage. Starting in the 1950s Mexico followed with government and bank-supported programs for wholesale removal of native vegetation replaced by monoculture buffelgrass stretching across vast swaths of the state of Sonora and elsewhere. This is one of the several most serious invasive species in the Sonoran Desert Region and poses a major threat in Organ Pipe and Cabeza Prieta (e.g., Rutman & Dickson 2002). Buffelgrass can carry fire, introducing a major threat to Sonoran Desert ecosystems that are not fire-adapted (e.g., Búrquez et al. 2002; Franklin et al. 2006). There are a number of strains selected for various traits, including increased forage value and frost tolerance, and some of these are patented.

OP: Near Growler Valley rain gauge, *Anderson 29 Oct 1984* (ORPI). 4 mi W of Bates Well, *Anderson 8 Mar 1986* (ORPI). Quitobaquito, 14 Sep 1988, *Felger 88-448*. W side of Sierra Santa Rosa, along border, 12 Mar 2003, *Felger 03-354*. Wash NE of Pinkley Peak, 31 Oct 2003, *Rutman 2003-1031-8* (ORPI). Growler Valley, "the few living plants are legacy of a very large population removed in the early 2000s," 8 Oct 2006, *Rutman 20061008-3*.

CP: 1 mi W of O'Neill's Grave, 11 Apr 1992, *Harlan 199* (CAB). Bassariscc Tank, 13 Jun 1992, *Felger* (observation). 2.5 mi S of Jose Juan Tank, 14 Sep 1992, *Felger 92-727*. Pinacate Lava, 1 mi E of Namer's Grave, sandy-silty loess over lava, 15 Sep 1992, *Felger 92-769*. Small wash near N end Agua Dulce Mts, 26 Sep 2013, *Rutman 20130926-19*.

TA: Tinajas Altas Mts, dirt road, 1986 (Van Devender et al. 1990: 339). Frontera Canyon, international border, not common, 18 Mar 1998, *Felger* (observation).

****Cenchrus echinatus** Linnaeus
Southern sandbur; *guachapori*. Figure 17.

Warm-weather ephemerals. Panicles spike-like to 7.5 cm long, with 18–40 burs. Burs often 4–5 mm diameter (not including spines), with a basal ring of often 30–50 small, slender bristles; larger spines flattened, 3.5–6 mm long.

Agricultural weed in the Sonoyta region and extending into the southern margin of Organ Pipe east of Lukeville. Not native to the region. It has not been relocated in Organ Pipe since the one collection, despite Rutman searching for it.

Unwelcome and often weedy from southern USA to South America and adventive in the Old World. *Cenchrus echinatus* and *C. spinifex* are separated on the basis of rather technical features.

OP: 0.5 mi E of Lukeville, 15–20 m N of border fence, locally common, 11 Nov 1987, *Felger 87-319*.

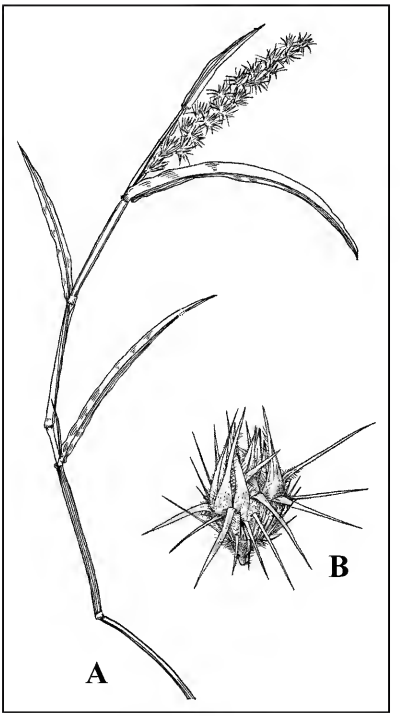

Figure 17. *Cenchrus echinatus*. (A) Culm, leaves, and panicle; (B) detached bur.

Cenchrus palmeri Vasey
Giant sandbur; *guachapori, huizapori*. Figure 18.

A unique grass with large, sharp-spined burs. Non-seasonal ephemerals, perishing with winter freezing; highly variable in size. Burs 1–3 per inflorescence, 20–31 mm in diameter, plus sharp stiff spines (6) 9–15 mm long, dark purple-brown most of the year, yellowish green during hot, humid weather. The obnoxious burs, the largest of any species of *Cenchrus*, persist long after the plant dies, often half hidden in the sand.

Widespread in northwestern Mexico especially on sandy soils including dunes in the Gran Desierto near the U.S. border. "This readily recognizable sandbur is one of the most distinct of the genus and is one of the very few grasses endemic to the Sonoran Desert" (Gould & Moran 1981: 123; also see Felger 2000). However, its range extends somewhat south of the Sonoran Desert along the coast to northwestern Sinaloa.

This species was not known to occur in the USA until 2013 when it was found in sandy soil about 15 km west of the flora area (Malusa et al. 2013). The sandy soils along the southern border in Cabeza Prieta and the Tinajas Altas Region are likely places for it to be found within the flora area. It apparently is advancing with the help of foot traffic including illegal border crossers (burs sticking to cloths and shoes) and vehicles (burs sticking to tires), and it is likely to spread into the flora area and on into the Yuma region.

Yuma County: Barry M. Goldwater Air Force Range, approx. 3 mi NW of Yodaville (Quad: West of Vopoki Ridge); UTM Zone 11, 7 46 608 E, 35 94 308 N, WGS 1984, 130 m, roadside at observation tower, and in nearby runnels, sandy flats, *Larrea, Palafoxia arida, Dalea mollis, Brassica tournefortii*, population estimate at 500–1000 plants, *Malusa & Sundt* 19 Jan 2013 (2 sheets, ARIZ 413972 & 413973).

Figure 18. *Cenchrus palmeri*. Dunes south of Sierra Blanca, Pinacate Biosphere Reserve, Sonora, 20 Feb 2010.

***Cenchrus setaceus** (Forsskål) Morrone
[*Pennisetum setaceum* (Forsskål) Chiovenda]
Fountain grass. Figure 19

Robust, tufted perennials to about 1 m tall. Culms erect to geniculate spreading. Leaves dull green and often reddish during cool weather. Leaf sheaths laterally compressed and keeled, glabrate to sparsely pilose with long slender hairs; hairs near collar usually sparse, white, and straight, reaching 5 mm with enlarged bases, the ligule membranous-ciliate. Leaf blades glabrate, scabrous, or sparsely pilose, especially on lower surface, larger blades 23–34 cm × 3–3.5 cm, the midrib prominent. Panicles feathery, 13–30 cm long, purplish especially during drier or cooler seasons and when young, and often whitish especially with age and during hot, humid times. Fascicles on slender, bristly stalks 1–2.5 mm long, fascicle bristles separate, flexible and somewhat sinuous, terete, unequal, the longer ones 22–34 mm and plumose basally. Spikelets 5.5–6.5 mm long, mostly on slender pedicels to 1 mm long, 1–4 per fascicle. Reproductive most of the year, especially during warmer months.

This Old World grass is often been planted as an ornamental garden subject in Ajo and Sonoyta and elsewhere in the Sonoran Desert Region, and has become a widespread invasive weed in desert areas of southern Arizona. It is naturalized in and around Ajo and is established on Childs Mountain and the Little Ajo Mountains. It was successfully eradicated along Hwy 85 through Organ Pipe in the 1990s but since then has been found at several very remote locations in the Ajo Mountains and foothills. It is abundant in Sonoyta, providing an invasion route into the Organ Pipe wilderness areas. It is a potentially serious invasive weed at waterholes, especially the disturbed habitats at

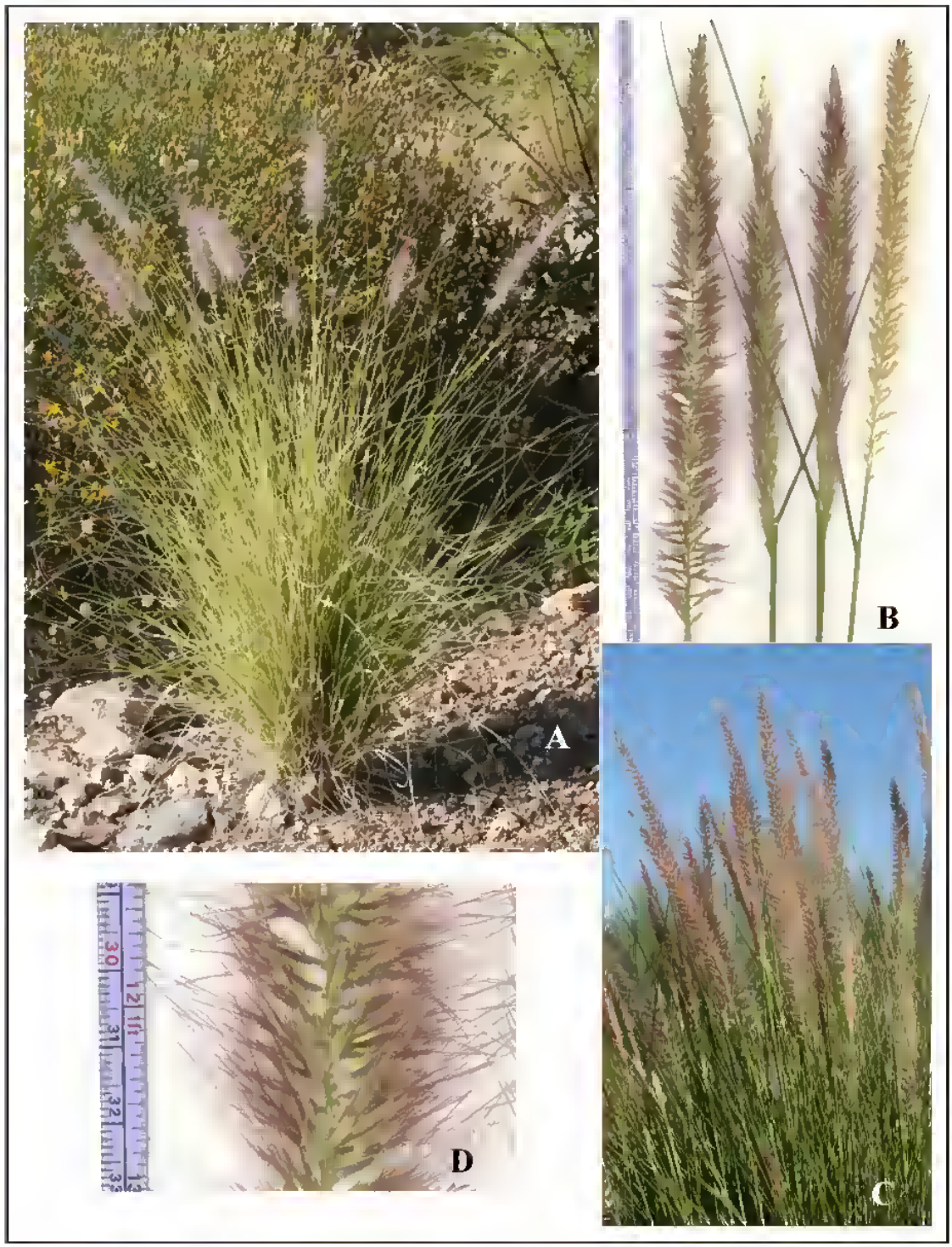

Figure 19. *Cenchrus setaceus*. Ajo, Pima Co (A) 14 May 2006, (B) 15 Sep 2013, (C) 12 Sep 2006, (D) 15 Sep 2013.

artificially enhanced waterholes, and could become a serious threat at higher elevations in the Ajo Mountains (Felger 1990).

Concerning fountain grass on Childs Mountain, Curtis McCasland (pers. comm. to R. Felger, October 2004) reported that he had a large and extensive population nearly eradicated. He observed it starting to spread down from the mountain top into drainages 1400–1700 ft and into an area to the west of Childs Mountain into Cabeza Prieta. It also extended into the Goldwater Range, but he had not seen there since 2002; it was about 1.5 mile east and a little bit north of the old officer's barracks on Childs Mountain (observed 15 Jul 2001, 0.1 acre of it seen with binoculars). Organ Pipe personnel have been eradicating fountain grass since the 1980s, when it was removed from several places along Highway 85. The largest known population was discovered in the southern Ajo Mountains in 2007 along a half km stretch of a rocky wash bed; in 2008 several hundred plants were eradicated from this site.

OP: 2 mi N of Visitor Center, *Anderson 18 Nov 1985* (ORPI). Hwy 85, vicinity of park headquarters, roadside, 11 Nov 1987, *Felger 87-333*. Alamo Canyon, ¼ to ½ mi downstream from junction of N and S forks, *Rutman 5 Mar 1995* (ORPI). Southern Ajo Mts, several hundred plants along a ¼ mile stretch of rocky wash bed, 10 Feb 2007, *Rutman* (observation).
CP: Childs Mt, 2300 ft, 18 Aug 1992, *Felger 92-646*

***Cenchrus spinifex** Cavanilles
[*C. incertus* M.A. Curtis. *C. pauciflorus* Bentham]
Common sandbur; *huzapori, guachapori*. Figure 20.

Warm-weather ephemerals or perhaps short-lived perennials with relatively deep and well-developed roots. Panicles compact and spike-like, 3.5–7 cm long, with 12–27 burs. Burs variable, 2.5–4 mm diameter (not including spines), shorter to longer than wide; spines mostly 8–40, very sharp, highly variable, long and slender to short and broad, the larger spines 4–5.7 mm long, the lower, smaller spines several and not in a basal ring.

Cabeza Prieta on the Pinta Sands near the Mexican border and nearby in similar habitat in Sonora several kilometers south of the international border (Felger 2000). Although highly localized, this population is apparently well established. This species was likely introduced into the flora area as a result of cattle grazing. The nearest records are from Yuma.

Southern USA to South America and the West Indies.

CP: 8 mi W of O'Neill's Grave, common in sand soil of a wash, 6 Mar 1977, *Reeder 6836*. E Pinta Sands, 6.5 mi W of O'Neill's Grave on Camino del Diablo, 15 Sep 1992, *Felger 92-758*.

Chloris virgata Swartz
Feather fingergrass; *zacate lagunero*. Figure 21.

Warm-weather ephemerals, 10–80 cm tall. Culms 1–many, often geniculate-spreading. Panicles with 4–17 spicate, unilateral branches at the top of the flowering stem, the branches ascending in a digitate pattern, the spikelets dense from the base, upright, whitish to tawny with silky hairs. Spikelets in two rows on the rachis, 2.8–3.5 mm long (excluding awns), with 2 differently shaped florets, each with a prominent awn. The lower floret fertile, the upper one sterile. Fertile lemma humpbacked on keel, bearing a conspicuous tuft of hair at the apex and a single stout awn 5–7.5 mm long. Sterile floret broad and truncate at apex, also bearing a single stout awn.

Figure 20. *Cenchrus spinifex*. (A) Lower Oak Creek, Sedona, Yavapai Co., photo by Max Licher, Jun 2001, from SEINet. Grant Co., NM, photos by Russell Kleinman, from Gilaflora.com: (B) Burro Mts, Mangas Canyon Road, 23 Jul 2007; (C) bur opened revealing a spikelet, Mangas Springs, 27 Aug 2009.

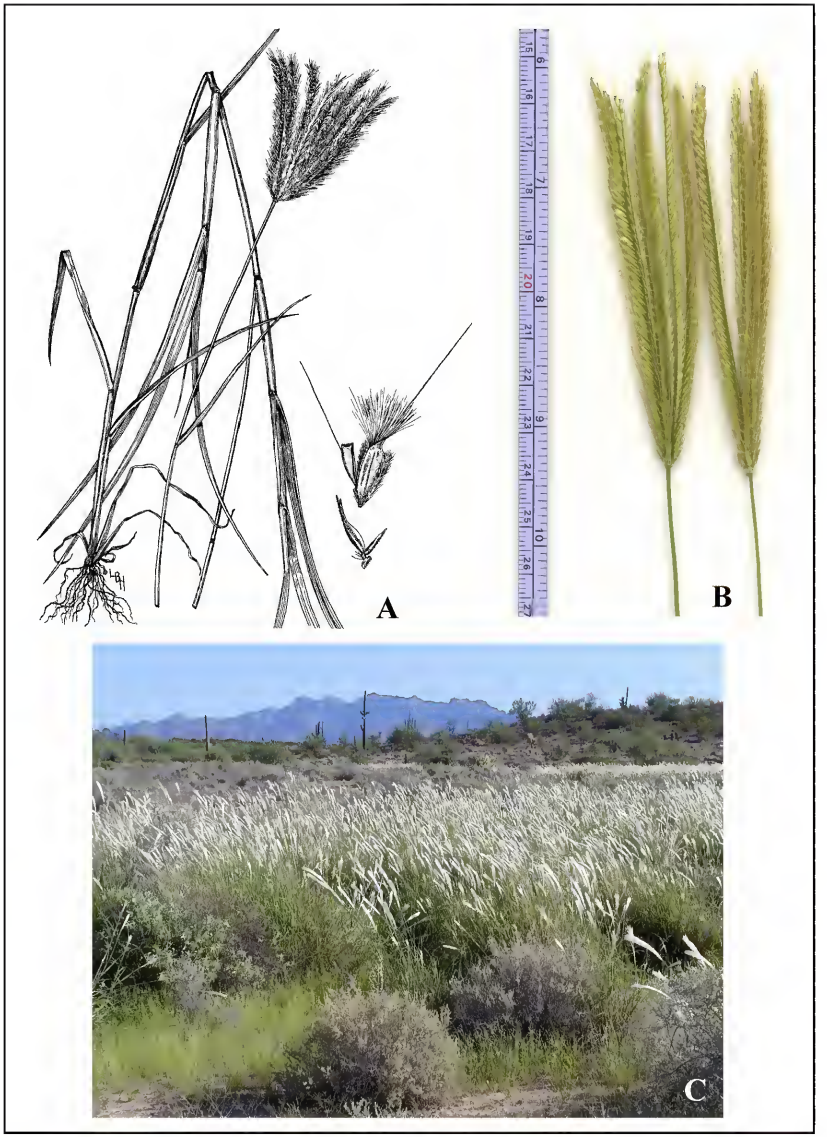

Figure 21. *Chloris virgata*. (A) Culms, roots, panicle, and spikelet with detached glumes and fertile and sterile florets. Near Dos Lomitas: (B) panicles, 11 Sep 2008; (C) dense, localized stands of exceptionally large plants, 29 Aug 2001.

Usually in sandy-silty soils in low-lying places, in natural habitats and often spreading from nearby disturbed habitats; locally common in the flora area at several widely scattered localities. For example, it is locally abundant in swales and eroded areas 1–2 miles east of Lukeville and north of the international border, co-occurring with Bermuda grass (*Cynodon dactylon*), buffelgrass (*Cenchrus ciliaris*), and blue panic grass (*Panicum antidotale*). Also found in Bull Pasture, Ajo Mountains.

Western USA to South America, and adventive in the Old World; often weedy.

OP: 0.5 mi E of Lukeville, 11 Nov 1987, *Felger 87-315*. Quitobaquito, 24 Oct 1990, *Felger 90-487*. Puerto Blanco Drive at 0.9 mi W of Hwy 85, 3 Dec 1990, *Felger 90-573*. Bull Pasture, 25 Sep 2013, *Rutman 20130925-3*.

CP: Monreal Well, *Simmons 21 Oct 1962* (CAB) Redtail Tank, 12 Jun 1992, *Felger 92-550*

Cottea pappophoroides Kunth
Cotta grass; *zacate papo*. Figure 22.

Tufted grasses, facultatively perennial or annual, often 30–75 cm tall, with well-developed, tough, wiry roots. Culms slender, often rather delicate and softly pilose, the basal nodes producing cleistogamous spikelets. Panicles terminal, open but rather narrow, the panicle branchlets, pedicels, and spikelets densely hairy. Spikelets with 6–10 florets; glumes multi-veined; lemmas 8–12-veined, the veins extending into 9 or more uneven, bristly awns. Growing with summer rains, reproductive in late summer and fall.

Occasional to sometimes common in the northern part of Organ Pipe and with other grasses on lower bajada and floodplain deposits of sandy loams along flat reaches of drainages, particularly in the Valley of the Ajo and one record from a similar habitat in Cabeza Prieta. Also localized and apparently rare on rocky slopes in the Ajo and Diablo Mountains.

Southwestern USA, northern and central Mexico to Oaxaca, and disjunct in South America.

The plants are facultatively winter and dry-season dormant, often (or usually?) dying back to the cleistogene-bearing bases. Although such plants, with their well-developed roots and knotty bases, appear perennial, they are often (or usually?) actually annuals regenerating from seeds in the basal cleistogenes. For example, the Cabeza Prieta specimen, collected in January 2002 long after the summer rainy season, appeared dead except for the cleistogenes. Similar facultative growth forms occur elsewhere, including the Sonoran Desert such as in the foothills of the Catalina Mountains (Jim Verrier, pers. comm. to R. Felger, February 2014) and in Argentina (Prof. Fernando Biurrun of Chamical, Argentina, pers. comm. to John R. Reeder, with subsequent pers. comm. to R. Felger 2002).

OP: N border of Monument, 11 Sep 1943, *Clark 10977* (ORPI) Armenta Ranch road, 1.4 mi W of Hwy 85 [Valley of the Ajo], 1 Feb 2002, *Felger 02-73*. Bull Pasture, *Rutman 30 Oct 1997* (ORPI) Foothills of Diablo Mts, W of Ajo Mt Drive, coarse colluvium, 778 m, rare, 22 Sep 2013, *Rutman 20130922-7*

CP: Papago Well, sandy bank of major wash, localized, fewer than one dozen plants seen, 11 Jan 2002, *Felger 02-38*.

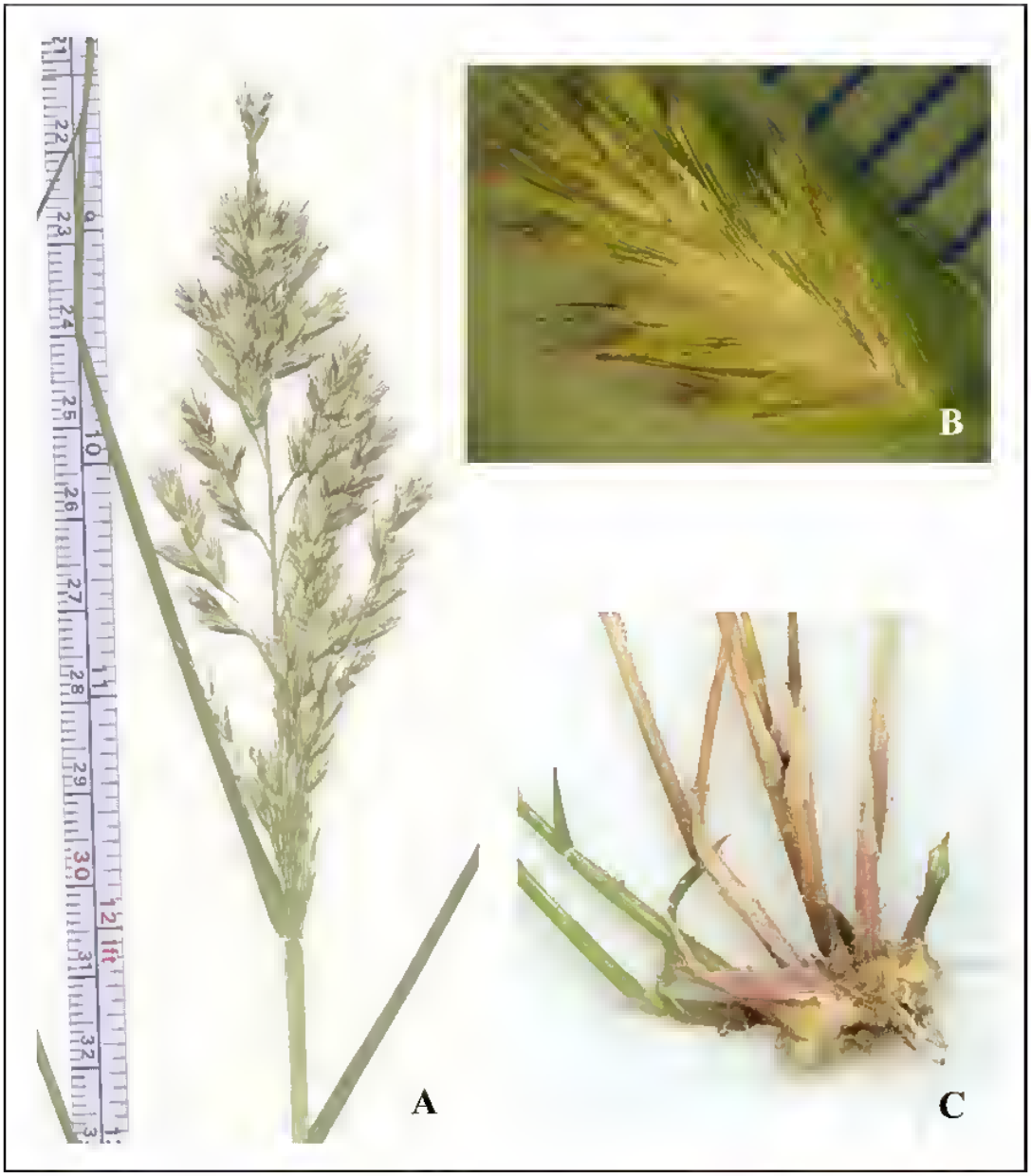

Figure 22. *Cottea pappophoroides* (A) Panicle, Diablo Mts, 22 Sep 2013; (B) spikelet, photo by Elizabeth Makings, from SEINet, (C) base of plant showing the swollen cleistogenes, Valley of the Ajo, W of Hwy 85 at mile marker 60, 3 Sep 2006

***Cynodon dactylon** (Linnaeus) Persoon var. **dactylon**
Bermuda grass, *zacate bermuda, zacate ingles*, ki weco vasai, 'a'ai hihimdam vasai. Figure 23.

Deeply rooted perennials with creeping, scaly rhizomes and long stolons, forming extensive mats. Leaves short, mostly 2-ranked. Inflorescence a panicle of 4–7 slender, digitately-arranged spicate, unilateral branches (2) 2.5–6 (8) cm long, purplish to green. Spikelets with 1 floret, (1.7) 2–2.5 mm long, (1.7) 2–2.5 mm long, awnless, numerous and crowded in two rows on one side of the triangular

rachis Actively growing and flowering during warmer months, and winter dormant unless protected from freezing weather.

Figure 23. *Cynodon dactylon*. (A) Plant, panicle, and enlargement of glumes, lemma and palea, and caryopsis. Alamo Canyon. (B) 6 May 2006, (C) 9 Sep 2008

Well established near springs, alkaline seeps, tinajas, and other waterholes where water may accumulate at least seasonally, in natural and disturbed habitats. Often at waterholes artificially "enhanced" or "improved" for wildlife. It can also occur in small or extensive patches in xeroriparian areas, along roadsides, and occasionally in uplands. It competes with *Distichlis spicata* and other native plants at Quitobaquito springs and has been at Quitobaquito at least since the early 1940s. *Cynodon* in 2013 covered several miles of xeroriparian area in Alamo Canyon. The upstream end is near the confluence of the middle and south forks of the canyon and extends several miles downstream. Perhaps it was planted or first established at or near the corral in Alamo Canyon.

Bermuda grass is the common summer lawn grass in the Sonoran Desert Region and also grown in irrigated fields for hay. There are a number of cultivated selections for turf grass and hay production. Native to the Old World and now a worldwide weed.

OP: Quitobaquito, 25 Mar 1941, *McDougall 36*. 0.5 mi E of Lukeville, 11 Nov 1987, *Felger 87-320*. Alamo Canyon, near corral, *Rutman 5 Sep 1999*.
CP: Observations Childs Mt, 2300 ft, abandoned military barracks, 18 Aug 1992, *Felger*. Eagle Tank, small colony at waterhole, 13 Jun 1992, *Felger*.

***Dactyloctenium aegyptium** (Linnaeus) Willdenow
Crowfoot grass; *zacate de cuervo*

Summer ephemerals; glabrous, the culms spreading to ascending or decumbent, often rooting at the nodes and forming radiating mats. Leaf blades flat, short, and thick. Inflorescence a panicle of (1) 2–6 thick and stubby, digitately arranged, spicate, unilateral branches 1.5–4.5 cm long, spreading at nearly right angles from top of the culm. Spikelets 2.7–3.5 mm long overlapping, with 3–5 densely crowded tiny florets, the naked rachis extending beyond the spikelets. Glumes unequal in size and shape; upper glume with an oblique awn 0.5–3.2 mm long just below the tip. Lemmas strongly keeled; lemma of the first floret 2.2–3.2 mm long, pointed or with a recurved awn less than 1 mm long. The fruit is an achene, which is unusual among the grasses in that the seed can be seen through the thin pericarp, which is soon shed. The seed is glistening red-brown and elegantly sculptured with thin, transverse, wavy, and evenly-spaced ridges, these ridges often dark brown or black and the sulci (minute valleys) lighter colored (reminiscent of the seed of *Mollugo cerviana*).

Known in the flora area by a single record in 1987, when it was locally common in wet soil beneath cottonwood trees at Quitobaquito. Common weed in the nearby Sonoyta Valley, especially in agricultural fields.

Native to the Old World and now nearly worldwide, mostly as a weed.

OP: Quitobaquito, 10 Nov 1987, *Felger 87-289*.

Dasyochloa pulchella (Kunth) Willdenow ex Rydberg
[*Triodia pulchella* Kunth. *Erioneuron pulchellum* (Kunth) Tateoka. *Tridens pulchellum* (Kunth) Hitchcock]
Fluff-grass; *zacate borreguero*. Figure 24.

Dwarf, tufted perennials 5–14 cm tall, sometimes flowering in the first season, with arching stolons of one internode, the longer ones 7–11 cm, bearing at their ends a tightly fascicled cluster of short leaves and inflorescences, often arching and bending to the ground and sometimes taking root and rarely producing a short, second stolon. Leaf blades 1.8–7 cm × less than 0.5 mm, minutely scabrous, the margins firm, in-rolled, and often white and thickened. Panicles densely white-pubescent, compact and densely flowered, on peduncles shorter than the longer leaves. Spikelets 6–

10 mm long, with (4) 6–8 florets, tardily breaking off above the glumes. Glumes and lemmas papery, sometimes purple-tinged, the glumes with a green midvein. Lemmas 3–5 mm long, densely pilose with long hairs on each of the 3 green veins, the lemma tip deeply 2-lobed with an awn 1–2 mm long from between the lobes. Flowering with warm weather and sufficient soil moisture, recruitment seems to generally occur with summer rains.

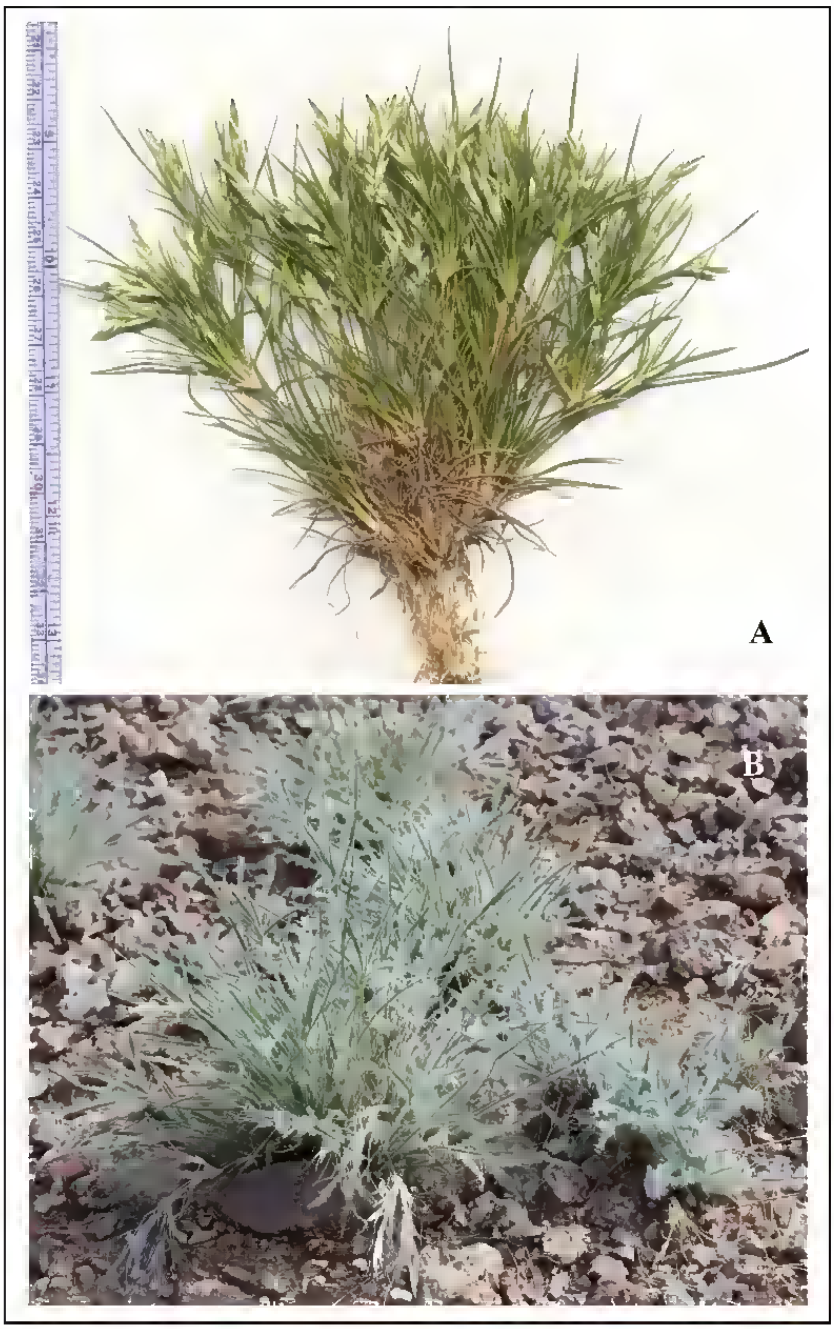

Figure 24. *Dasyochloa pulchella*. (A) Adult plant, Why, Pima Co., 15 Apr 2013, (B) Young leaves with bluish gray indumentum of hair-like crystals, between Boulder and Estes Canyons, Ajo Mts, 2 Aug 2013.

An impressively large pulse of recruitment occurred in Organ Pipe during summer 2012, a year with exceptionally high summer rainfall. Young plants and sometimes young leaves appear bluish gray or whitish: seedlings "are shaggy-white-villous. The indumentum is composed of myriads of hair-like, water-soluble crystals that wash off in water. They are the product of transpiration and evaporation" (Valdés-Reyna 2003: 47; Figure 24B). During the driest times the drought-killed aerial part of the plants persist, acting to shelter emerging shoots in subsequent favorable seasons, or the entire plant may die and apparently function as a nurse plant for seedlings at a later time. This grass is one of the most arid-inhabiting perennial grasses in the Sonoran Desert.

Widespread across the flora area in dry, open habitats including bajadas, hills, and mountains. It has been widespread across the region for more than 11,250 years.

Arid and semi-arid southwestern USA and northwestern Mexico and the Chihuahuan Desert Region.

OP: N border of Monument, 11 Sep 1943, *Clark 10982* (ORPI). Ajo Mt Drive 6.7 mi NE of Visitor Center, 5 Sep 1977, *Bowers 921*. Quitobaquito, 10 Nov 1987, *Felger 87-290*. Residence area, 30 Mar 1988, *Felger 88-142*. 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-11*. Between Boulder and Estes Canyons, along Ajo Mt Drive, 2 Aug 2013, *Rutman 20130802-2*. †Puerto Blanco Mts, 30 to 9070 ybp (13 samples, Van Devender et al. 1990: 339).

CP: Charlie Bell Pass, 3 Apr 1992, *Whipple 3937* (CAB). Childs Mountain, 18 Aug 1992, *Felger 92-641*. Scarface Mt, S-facing slope, 1750 ft, *Autenreith 20 Mar 1992* (ASC). Agua Dulce Pass, Heart Tank, Senita Tank, 13 & 14 Jun 1992, *Felger* (observations).

TA: Camino del Diablo SE of Raven Butte, 26 Nov 2004, *Felger 04-11*. Tinajas Altas, above upper tinajas, 26 Nov 2004, *Felger 04-92*. †Butler Mts, 220 to 11,250 ybp (9 samples, Van Devender et al. 1990: 342). †Tinajas Altas Mts, 4010 to 10,300 ybp (5 samples, Van Devender et al. 1990: 340).

Digitaria californica (Bentham) Henrard var. **californica**
[*Trichachne californica* (Bentham) Chase]
Arizona cottontop; *zacate punta blanca*. Figure 25.

Tufted perennials 50–90 cm tall, winter or dry-season dormant from a hard, knotty base. Culms firm, with felt-like hairs. Blades of larger leaves 12–17 cm × 4–6.5 mm. Panicles narrow, with 5–10 erect and densely-flowered branches. Spikelets panicoid; paired, one long-pedicelled, the other much shorter, or the second spikelet on portions of a branch sometimes not developing. Spikelets 2.5–5 mm long (excluding the hairs). Lower glume minute, the upper glume slightly narrower and shorter than the sterile lemma. Upper glumes and sterile lemmas each with 3 major veins in addition to the marginal and obscure veins, and densely pubescent with silky-cottony white to pale purplish marginal hairs overtopping and mostly covering the spikelet. Fertile lemmas with thin flat margins, the margins not inrolled (unlike many other panicoid grasses).

Arroyos, canyons, and rocky slopes, and along washes and on sandy loam. Widespread in Organ Pipe and especially common in the north-central part. It is favored by cattle and likely declined in much of the flora area during the cattle-grazing period. Also widespread in Cabeza Prieta and rare at Tinajas Altas. It has been in the Ajo and Puerto Blanco Mountains for at least 20,500 years. A spikelet from the oldest packrat midden is amazingly preserved, complete with dense, silky white hairs and a reduced lower glume.

Colorado to Texas and Arizona, rare in California, and southward to Puebla, the Caribbean, and South America. An additional variety, var. *villosissima* Henrard, occurs in South America and the Caribbean.

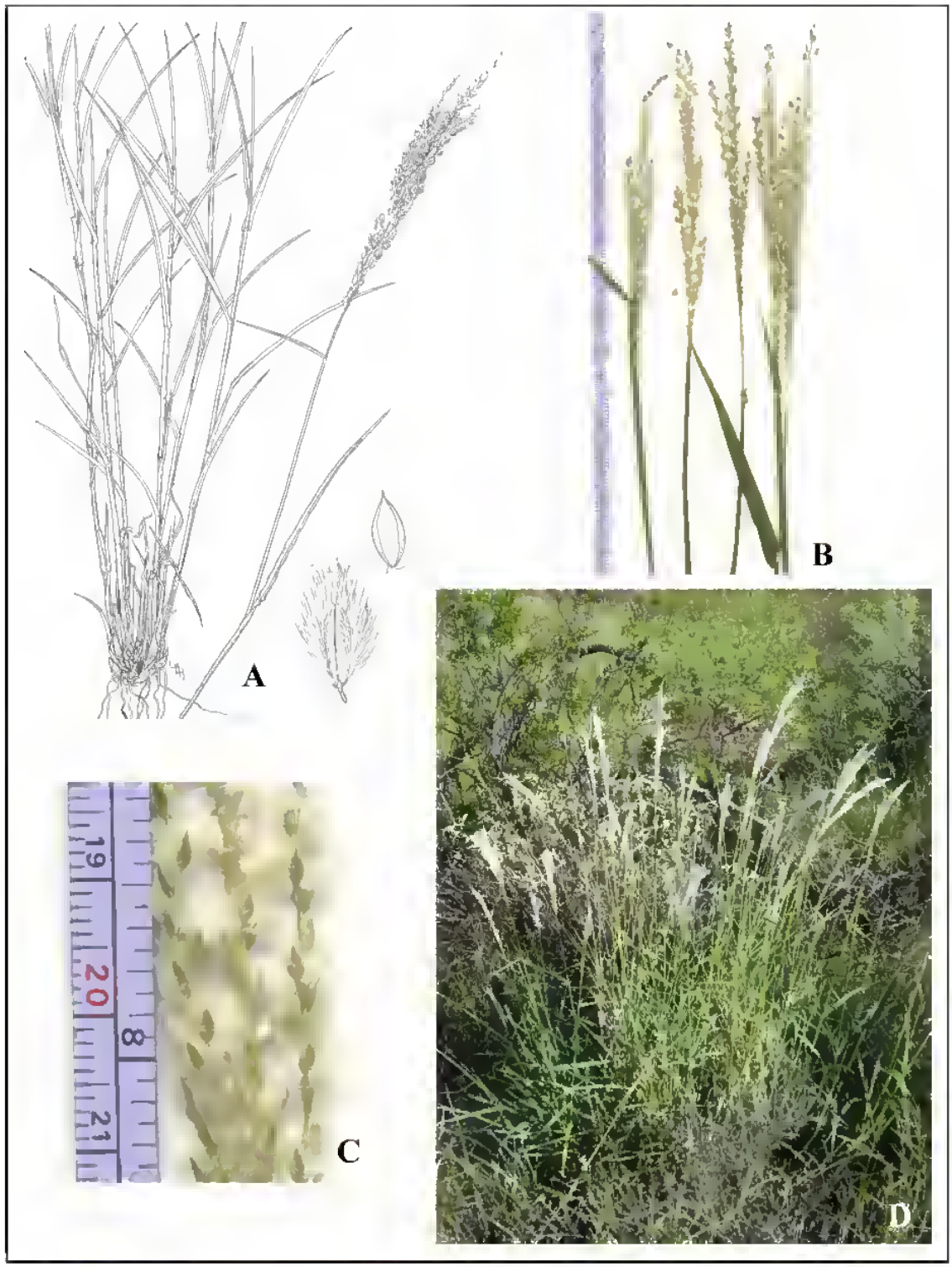

Figure 25. *Digitaria californica*. (A) Plant, culm with panicle, spikelet, and fertile floret, (B & C) panicles and spikelets, Why, Pima Co., 15 Sep 2013, (D) Diablo Mts, 14 Sep 2013.

OP: Alamo Canyon, *Nichol 4 May 1939*. Ajo Mt Drive 6.7 mi by road NE of Visitor Center, 5 Nov 1977, *Bowers 923*. Quitobaquito, 24 Oct 1990, *Felger 90-484*. About 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-2*. †Alamo Canyon, florets, 8590 & 9570 ybp. †Montezuma's Head, spikelet, 13,500 & 20,490 ybp. †Puerto Blanco Mts, 7560 to 7970 ybp (3 samples, Van Devender et al. 1990: 339).

CP: 6 mi E of Papago Well, 15 Nov 1936, *Goodding 924G*. Pinacate Lava, E of Namer's Grave, 15 Sep 1992, *Felger 92-771*. Agua Dulce Tank, Buckhorn Tank, 13 & 14 Jun 1992, *Felger* (observations). Childs Mt, 9 Apr 1993, *Felger 93-278*.

TA: Tinajas Altas, among rocks at base of tinaja slopes, 28 Mar 2010, *Felger 10-185*.

Dinebra

Annuals/ephemerals (sometimes stout and appearing perennial), the stems erect or geniculate-ascending. Ligule membranous. Inflorescences panicles of many racemose, unilateral branches bearing few to many spikelets. Spikelets packed broadside to the rachis, appressed, with 1–4 fertile florets and reduced florets above, laterally compressed, and breaking apart at maturity. Glumes persistent and exceeding the florets. Fertile lemma 3-veined, unawned or with a mucro (short bristle).

Dinebra includes 23 species widely distributed in the New and Old Worlds (Peterson et al. 2012; Snow & Peterson 2012).

1. Lemmas awnless ..... **Dinebra panicea**
1. Lemmas short-awned ..... **Dinebra viscida**

Dinebra panicea (Retzius) P.M. Peterson & N. Snow subsp. **brachiata** (Steudel) P.M. Peterson & N. Snow
[*Leptochloa brachiata* Steudel. *L. filiformis* (Persoon) P. Beauvois. *L. panicea* (Retzius) Ohwi subsp. *brachiata* (Steudel) N.W. Snow]
Red sprangletop; *deparramo rojo*. Figure 26.

Summer ephemerals, usually delicate and filmy; sometimes reaching 50+ cm tall but usually much smaller; green or sometimes reddish maroon. Roots often weakly developed. Glabrous or the leaf sheaths sparsely hispid with bulbous-based hairs. Spikelets 2.2–3.2 mm long, with (1) 2 or 3 florets, the mature (grain-bearing) spikelets sometimes appearing to have 1 floret. Glumes generally shorter than the rest of the spikelet; lemmas awnless, the veins, especially the midrib, often sparsely pubescent with small soft hairs, or sometimes glabrous or essentially so.

Often common along watercourses or floodplains, washes and canyon bottoms, margins of dirt tanks, playas, and depressions in silty-sandy soils; widespread in lowland areas.

Subspecies *brachiata* occurs in southern half of the USA to South America. It is often weedy and is introduced and spreading elsewhere in the world.

This grass was long known as *Leptochloa filiformis*, then *L. mucronata* (Michaux) Kunth, and then as *L. panicea* subsp. *mucronata* (Michaux) Nowack, and most recently as *Dinebra panicea* subsp. *brachiata*. Subspecies *mucronata* is restricted to southeastern and central USA, and subsp. *panicea* is native to the Old World (Peterson et al. 2012).

OP: Alamo Canyon, *Van Devender 31 Aug 1978*. Ajo Mt Drive, 12 Sep 1978, *Bowers 1518*. Aguajita Wash, 14 Sep 1988, *Felger 88-402*. 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-8*.

CP: Monreal Well, *Simmons 21 Oct 1962* (CAB). Jose Juan Represo, 12 Jun 1992, *Felger 92-564*. E of Namer's Grave, 15 Sep 1992, *Felger 92-773*. San Cristobal Wash, 14 Sep 1992, *Felger 92-691*. Las Playas, 28 Nov 2001, *Felger 01-562*.

Figure 26. *Dinebra panicea*. Alamo Canyon: (A) 9 Sep 2013; (B) 15 Sep 2013. (C) Growler Canyon, Bates Mts, 8 Sep 2006.

Dinebra viscida (Scribner) P.M. Peterson & N. Snow
[*Leptochloa viscida* (Scribner) Beal]
Sticky sprangletop. Figure 27.

Scruffy little summer-fall ephemerals often 10–30 cm tall, but stunted plants can reproduce as small as 1.5 cm tall. The viscid-sticky feature is often used as a key character, but the plants are often only scarcely viscid. You can usually find a few sparkling droplets on the flowering axes and branches, and this exudate is sometimes thick on the lemmas. Roots often poorly developed. Culms often forming short, geniculate ("bent-knee") and spreading branches, these sometimes forming roots at the nodes. Panicles at first often partially enclosed in the leaf sheath, later expanding and

spreading. Spikelets with several florets. Glumes and lemmas thin, glumes with a prominent green midvein. Lemmas 2–2.8 mm long, with a rounded, notched apex, and 3 prominent green veins with the midrib extending into a slender awn to 1 mm.

Seasonally abundant in the large playas in Cabeza Prieta and similar habitats in nearby northwestern Sonora.

Southern California to western Texas, both Baja California states, Chihuahua, Sonora, and Sinaloa.

CP. Las Playas. 10 Oct 1958, *Monson 7*, 28 Nov 2001, *Felger 01-561*.

Figure 27. *Dinebra viscida*. (A) Plant, culm with panicles, and spikelet and caryopsis, (B) spikelet, photo by Elizabeth Makings, from SEINet

Diplachne fusca (Linnaeus) P. Beauvois ex Roemer & Schultz subsp. **uninervia** (J. Presl) P.M. Peterson & N. Snow
[*Diplachne uninervia* (J. Presl) Parodi. *Leptochloa uninervia* (J. Presl) Hitchcock & Chase. *L. fusca* (Linnaeus) Kunth subsp. *uninervia* (J. Presl) N. Snow]
Mexican sprangletop. Figure 28.

Figure 28. *Diplachne fusca* subsp. *uninervia*. (A) Plant, panicle, and spikelet; (B) panicles, Gila River Canal at Buckeye, Maricopa Co., 31 Mar 2013.

Robust annuals, often appearing perennial, often forming large clumps 0.5+ m tall, non-seasonal but responding best to hot weather. Herbage and inflorescences glabrous or minutely scabrous. Inflorescences panicles with many narrow, racemose branches. Spikelets generally dark grayish green ("lead-colored," or sometimes pale rose-colored when immature), 4.2–6.4 mm long with 4–8 florets. Lemmas obtuse to truncate, awnless or with a minute awn in the terminal notch.

Infrequent in alkaline/saline, wet soils in the vicinity of Quitobaquito and the sandy-loam grassy flats along the Armenta Road.

Often in wetland habitats in the Sonoran Desert Region. Subspecies *uninervia* ranges from southern USA to Argentina, Chile, Peru, and the Caribbean. The *Diplachne fusca* complex includes 3 subspecies in addition to subsp. *uninervia*: *D. fusca* subsp. *fascicularis* (Lamarck) P.M. Peterson & N. Snow is widespread in the Americas, and the other two are native to the Old World.

OP: Sonoyta River near Quitovaquito, 30 Jan 1894, *Mearns 2741* (US). Rincon Spring, 13 Apr 1941, *McDougall 89*. Williams Spring, *Van Devender 30 Aug 1978* (ORPI). Armenta Rd, *Rutman 16 Aug 2001* (ORPI). Below Cement Tank, Santa Rosa Mts, 2 Apr 2003, *Rutman 2003-442*.

Disakisperma dubium (Kunth) P M. Peterson & N. Snow
[*Diplachne dubia* (Kunth) Scribner. *Leptochloa dubia* (Kunth) Nees]
Green sprangletop. Figure 29

Tufted perennials, 40–100 cm tall, often purple-tinged and with a tough, knotty base, sometimes reproductive in the first season or year. Ligule a membrane fringed with white hairs. Larger leaf blades 25–36 cm long, often somewhat bluish green. Enlarged, cleistogamous spikelets often at culm bases. Panicles 18–24 cm long, with several or more unbranched, racemose primary branches, the branches triangular in cross section. Florets of young spikelets crowded but at maturity become well separated and the rachis becomes readily visible. Spikelets with 5–12 florets. Spikelets breaking apart above the glumes and between the florets, each floret falling with its segment of rachis. Lemmas 2.1–5 mm long, 3-veined, broadly truncate (blunt-ended), with 2 broad lobes and the midrib extending into a slender bristle within the notch.

In the flora area known from the Ajo Mountain, at middle to higher elevations, and in 2013 seen along Kuakatch Wash about 1 mile west of Highway 85.

Arizona to Oklahoma and Texas, Florida, Mexico including Baja California to Central America, and South America.

OP: Main canyon N of Alamo Canyon, 3600 ft, 31 Mar 1948, *Gould & Darrow 4690*. Bull Pasture Trail, 2800 ft, *Henry 26 Sep 1976* (ORPI). Arch Canyon, 900 m, 2 Dec 1990, *Felger 90-538* (ORPI). Kuakatch Wash near E boundary of the Monument, 10 Sep 2013, *Rutman* (observation).

Figure 29. *Disakisperma dubium*. (A) Plant, panicle, and spikelet, (B) panicles, Alamo Canyon, 15 Sep 2013.

Distichlis spicata (Linnaeus) Greene
[*D. stricta* (Torrey) Rydberg]
Saltgrass; *zacate salado*; 'onk, vasai. Figure 30.

Perennials with creeping rhizomes, forming extensive colonies. Leaves 2-ranked, with salt-excreting bicellular hairs sunken in leaf tissue; ligules minute and membranous; leaf blades mostly 4–8 cm long, mostly firm and sharp-pointed (softer and not sharp-pointed when growing in shade with ample water). Inflorescence a slender, few-branched panicle or raceme; staminate and pistillate flowers on separate plants; staminate inflorescences usually overtopping the leaves, pistillate inflorescences about as tall as the leaves. Spikelets mostly 5–15 mm long, soon becoming straw-colored, laterally compressed, awnless, with few to many florets. Winter dormant; growing and reproductive during the warmer months.

In the flora area only known from the Quitobaquito region where it is locally abundant on moist to wet, hypersaline soils where perennial water is at or near the surface. When cattle were being grazed at Aguajita the wash near the spring was open and there was a perennial flow. After the cattle were removed in the late 1970s the local flora changed rapidly in response to the changing habitat: *Distichlis* increased and crowded out other plants, and subsequently the *Distichlis* declined as it was crowded out by arrow-weed (*Tessaria sericea*) and mesquite trees. A significant flood in the summer of 2012 once again opened the Aguajita wash bed allowing increase in the *Distichlis*. Extensive local populations occur at Quitobaquito Spring and Williams Spring, and a small population is at Burro Spring.

Coasts and interior basins; Canada to Mexico, the West Indies, and southern South America.

OP. Quitobaquito, *Nichol 28 Apr 1939*. Williams Spring, 13 Sep 1986, *Felger 86-274*. Aguajita Wash, 14 Sep 1988, *Felger 88-442*. Quitobaquito Spring, saline, crusty, sandy soil, *Glenn 26 May 1990*. On berm that creates Quitobaquito Pond and common on hypersaline soils seasonally wetted by springs, soil pH exceeding 10, with *Schoenoplectus americanus*, 15 Jun 2013, *Rutman 20130615-1*

Echinochloa – Barnyard grass

Annuals (in the flora area). Ligules absent (those in the flora area, this being the only grass genus in the flora area without ligules). Leaf blades with a prominent midrib. Panicles terminal, with few to many spike-like branches. Spikelets panicoid, densely crowded in 2 or 4 crowded rows on one side of a flattened rachis, breaking off below the glumes, with 2 florets, the lower one sterile and reduced or staminate, the upper one bisexual. Lower glume short, the upper glume similar to the sterile lemma. Fertile lemma smooth, shiny, and flat, with margins covering a flat palea of similar texture.

1. Leaf blades with transverse purple bars or blotches; hairs or bristles (spines) on spikelets, panicle axes, and branches not bulbous-based; spikelets 2.2–2.6 (3) mm long, awnless; panicle branches 1–2 (3) cm long, simple ..... **Echinochloa colona**
1. Leaves uniformly green, without purple markings; hairs and bristles on spikelets and panicle axis and branches often bulbous-based; spikelets 2.8–4 mm long (excluding awns and projections), often but not always long-awned; panicle branches usually 2.5–6 cm long, usually with at least some short secondary branches ..... **Echinochloa crus-galli**

***Echinochloa colona** (Linnaeus) Link
Jungle rice, leopard grass; *zacate pinto, zacate tigre, zacate rayado*. Figure 31.

Summer ephemerals and sometimes occurring with warm weather at other seasons. Leaf blades with transverse purple bars or blotches—no other grass in Arizona and the Sonoran Desert has

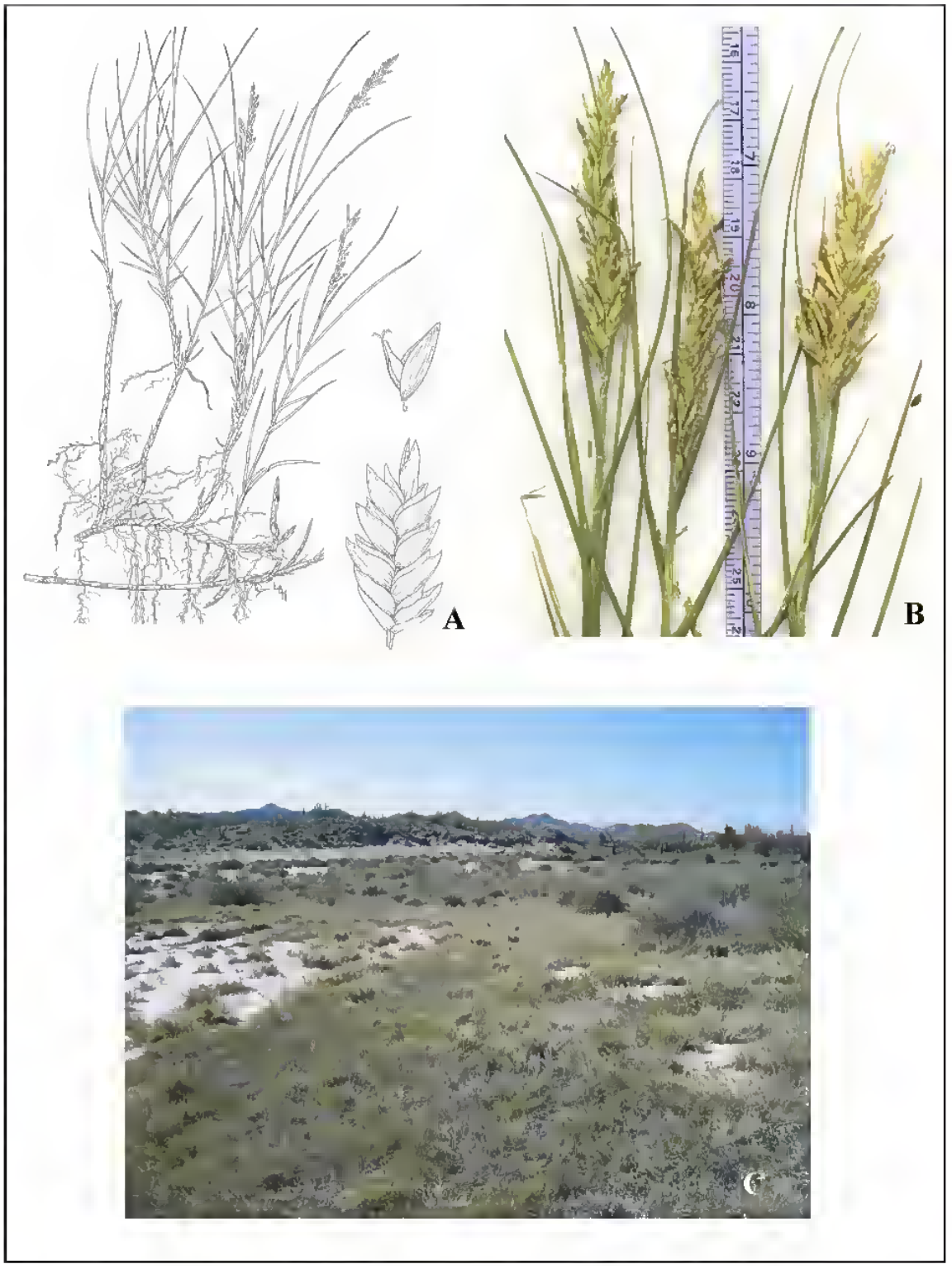

Figure 30 *Distichlis spicata.* (A) Plant with panicles, spikelet, and pistillate floret; (B) pistillate panicles, Quitobaquito Pond, 16 Jun 2005; (C) Williams Spring, 4 Feb 2005

these markings. Panicle branches simple, 1–2 (3) cm long, panicle branches and spikelet hairs not bulbous-based Spikelets in 4 rows, awnless, 2.2–2.6 (3) mm long Lower florets sterile, or perhaps sometimes staminate.

Mostly in wet soil at waterholes including margins of dirt tanks and temporary wetland habitats such as arroyo bottoms, sometimes in wet soil at disturbed habitats Also observed in 2012 below a chronically dripping faucet at the maintenance facility in Organ Pipe

Native to the Old World, now widespread and mostly weedy in tropical and subtropical regions worldwide

OP Williams Springs, *Van Devender 31 Aug 1978* (ORPI) Ajo Loop Rd 2 mi NE of Visitor Center, 9 Sep 1984, *Van Devender 84-451* 0.5 mi E of Lukeville, 11 Nov 1987, *Felger 87-323* Maintenance area, NPS headquarters, *Casper 24 Mar 2003*

CP Redtail Tank, 12 Jun 1992, *Felger 92-549* Jose Juan Tank, 14 Sep 1992, *Felger 717* San Cristobal Wash, deep shade under *Prosopis*, 26 Sep 2013, *Rutman 20130926-8*

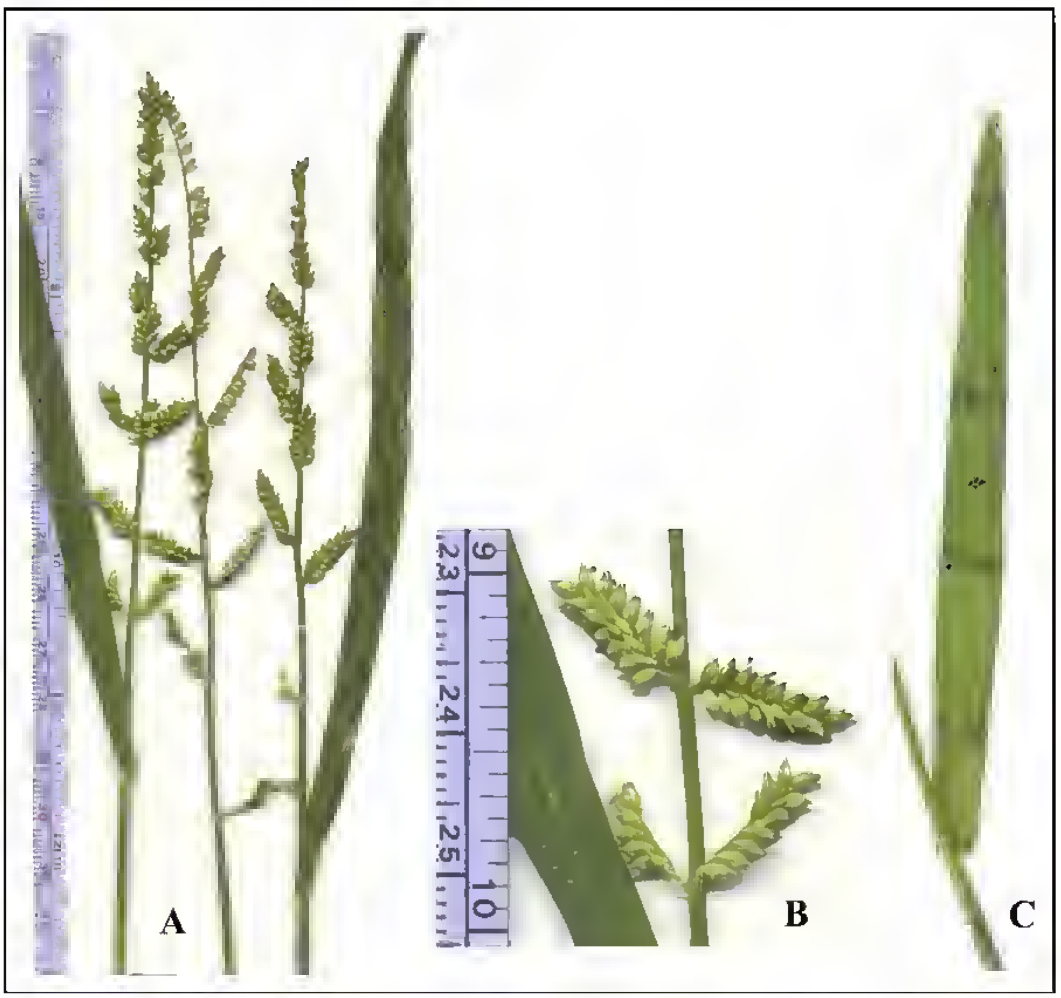

Figure 31 *Echinochloa colona* (A & B) San Cristobal Wash at Camino del Diablo, 26 Sep 2013; (C) Alamo Canyon near Alamo Well, 21 Oct 2007.

Echinochloa crus-galli (Linnaeus) P. Beauvois
Barnyard grass, *zacate de agua, zacate de corral*. Figure 32.

Coarse, warm-weather annuals, the plants often more robust than those of *E. colona*. Leaf blades uniformly green, the larger ones mostly 1–1.5 cm wide. Panicle branches mostly 1–4 cm long (to 9 cm elsewhere in better watered places), the larger branches sometimes with short secondary branches, branches and main axis of panicles with stout, often bulbous-based bristle-like hairs. Spikelets 2.8–4 mm long, awned or awnless, even on the same plant and within the same panicle, the awns highly variable in length, often purplish, the longer awns 2.6–5.8 cm. Lower florets sterile, with a well-developed palea. (Description based on the one local specimen and ones from adjacent desert areas.)

Known from the flora area by a single record. Locally common in nearby Sonora in the vicinity of Sonoyta in seasonally wet mud along the riverbed, irrigation ditches, and at water impoundments.

Native to the Old World, now weedy and adventive nearly worldwide.

CP. Jose Juan Represo, 12 Jun1992, *Felger 92-558*.

Figure 32. *Echinochloa crus-galli*. (A) Plant with panicles, open spikelet showing the small lower glume (bottom), upper glume (right), sterile lemma with smaller sterile palea (left), and fertile lemma and palea enclosing the caryopsis (center), fertile floret (center), two views of awned spikelet (above), (B) spikelets, photo by Elizabeth Makings, from SEINet.

Elymus elymoides (Rafinesque) Swezey var. **brevifolius** (J.G. Smith) Dorn
[*Sitanion hystrix* (Nuttall) J.G. Smith var. *brevifolium* (J.G. Smith) C.L. Hitchcock. *Elymus longifolius* (J.G. Smith) Gould]
Bottlebrush squirrel-tail, *triguillo desértico*. Figure 33.

Tufted perennials, without rhizomes. Leaf sheaths bear a pair of slender, fang-like auricles (like many *Hordeum* species); ligules minute. Inflorescence a spike 8–15 cm long (not including awns), densely flowered, and bristly with stout, scabrous awns mostly 2.5–12 cm long on glumes and lemmas. Spikelets usually paired at nodes, usually with 2–4 florets per spikelet, the lower floret fertile; glumes bristle-like. At maturity the inflorescences break apart in segments that roll away like miniature tumbleweeds. Grain linear-oblong, furrowed in back, adhering to the palea.

Ajo Mountains, mostly on rocky slopes at higher elevations—it extends no farther west into the desert. This or a similar grass has been in the Ajo Mountains for more than 29,000 years.

Widespread in Arizona, generally at elevations above the desert. This species, with 4 subspecies, occurs in western North America from Canada to Mexico. In the flora is var. *brevifolius*, which ranges farther south than the other subspecies and occurs from northwestern Mexico to Canada (Barkworth et al. 2007c). Taxonomy of the squirrel-tail grasses is complicated (see Allred & Ivey 2012).

OP: Alamo Canyon, *Nichol 4 May 1939*. Arch Canyon, 3 May 1978, *Bowers 1302*. Trail from The Cones to Mount Ajo, 3940 ft, 10 Apr 2005, *Felger 05-262*. †*E.* cf. *elymoides*. Alamo Canyon, florets, 9570 to 29,110 ybp (3 samples); Montezuma's Head, 13,500 to 21,840 ybp (4 samples).

Figure 33. *Elymus elymoides* var. *brevifolius*. Fay Canyon, west of Sedona, Yavapai Co., 8 May 2004, photo by Max Licher.

Enneapogon – Pappus grass

Tufted annuals or perennials, generally with soft, glandular hairs. Panicles slender and spike-like, overtopping the leaves, feathery, and with soft hairs Spikelets with 2 or 3 florets, usually only the lower one bisexual. Lemmas rounded on the back, prominently 9-veined, the veins extending into 9 feathery awns, usually dark-colored—making this grass unmistakable (*Enneapogon* is derived from the Greek words for nine beards).

1. Robust annuals (may appear perennial), culms 2 mm wide, not forming cleistogenes, panicles 1–3 cm wide ..... **Enneapogon cenchroides**
1. Small perennials, culms to 1 mm wide, with well-formed cleistogenes at their bases, panicles usually to 1 cm wide ..... **Enneapogon desvauxii**

***Enneapogon cenchroides** (Lichtenstein ex Roemer & Schultes) C.E. Hubbard
Soft-feather pappus grass. Figure 34.

Figure 34. *Enneapogon cenchroides*. (A) King Canyon, Tucson Mts, Saguaro National Park, 9 Oct 2011, photo by Anthony Mendoza, from SEINet, (B) panicle, east Broadway Blvd., Tucson, 17 Oct 2007

Robust annuals (often appearing perennial, probably non-seasonal annuals), (20) 35–70+ cm tall, roots strong and with conspicuous root hairs and rhizosheaths. The lower culms finely pilose. Panicles (5) 9–24+ cm long, 1–2 (3) cm wide, densely flowered and often dark-colored. Reproductive September to December or January.

Found at Alamo Canyon in the 1990s and later at an isolated hill west of the Diablo Mountains. It will probably spread and could become seriously invasive at higher elevation in the Ajo Mountains.

Introduced in the Tucson region and well established in the Catalina Mountains in Pima County at least since 1976 and documented since the 1980s in other scattered Arizona localities. Since the 1990s populations in the Tucson Basin have rapidly expanded and Rutman observed it in 2012 along Highway 86 on the eastern part of the Tohono O'odham Reservation. Locally established in desert, grassland, and oak woodland, sometimes with extensive populations in Cochise, Graham, and Pima Counties. Native to the Old World, in Africa and Madagascar to India.

This Old World grass might be confused for the native *Pappophorum*. *Enneapogon* has feathery (plumose) awns, while *Pappophorum* has scabrous (rough) but not plumose awns and narrower leaves. *Enneapogon cenchroides* panicles tend to be narrower and darker colored than those of *Pappophorum*.

OP. On a small, inconspicuous hill about 4–4.5 mi by road from the Visitor Center on the Ajo Mountain Drive, hill is SE of road: 24 Sep 2006, *Rutman 20060924-1*; 22 Oct 2006, *Rutman 2006-1022-1*.

Enneapogon desvauxii P. Beauvois
Spike pappus grass, nine-awn pappus grass; *zacate lobero*. Figure 35.

Small, tufted perennials or sometimes functionally annuals, often 15–20 (30) cm tall, with hard, knotty bases containing cleistogamous, awnless spikelets. Leaf sheaths and lower parts of the culms finely pilose. Ligules a row of hairs, these about 1 mm long. Leaf blades wiry, less than 10 cm × 0.5 (1) mm, the margins in-rolled during drier times, and flat and reaching 1.5 mm wide during moist times (e.g., with summer–fall rains). Panicles spike-like, terminal, slender, and densely flowered. Spikelets 4.5–7 mm long including awns, lead-gray or gray-green, mostly 3-flowered, only the lower one bisexual. Glumes subequal, sparsely and finely pubescent, with well-marked green veins plus 1 or 2 faint ones, the lower glume 5–7-veined, the upper glume 3–4-veined. Lemmas with dark-colored feathery awns, the longer awns 3–4.5 mm. Grain 0.8–1.2 mm long with an abruptly narrowed tip 0.1 mm long, golden- to tan-colored, plump and ovoid or oval. Cleistogamous spikelets buried in the lower part of the leaf sheaths at the stem bases, the stems breaking off "at the lower nodes, carrying the cleistogenes with them" (Hitchcock 1951: 227). Cleistogamous florets lack glumes and awns, the grain resembling the chasmogamous ("normal") grain but larger (1.8–1.9 mm long) and at maturity splitting the sheath in which it develops.

The plants sometimes produce short culms with reduced panicles bearing spikelets with short-awned florets that are intermediate between the cleistogamous and chasmogamous florets. Sometimes the plants perish in drought but remain intact, and in subsequent rainy seasons new plants germinate from cleistogenes at the base of the dry, dead mother plant, which functions as a nurse plant—the plants thus being functionally annual. Also see *Cottea pappophoroides*.

Arid rocky and rocky-gravelly soils in hills and mountains. Widely scattered in Organ Pipe and on the eastern side of Cabeza Prieta.

Southwestern USA to Oaxaca, South America, and the Old World.

OP. Near Pozo Nuevo, 12 Feb 1978, *Bowers 1053*. Near mouth of Arch Canyon, 2 Dec 1990, *Felger 90-524* (ORPI). Eagle Pass, *Wrt 16 Sep 1990* (ORPI). Saddle between Arch and Boulder Canyons, *Rutman 24 Sep 1998* (ORPI). Gunsight Hills, 3557286N, 342604E, biotite granite bedrock or thin soil, 27 Sep 2006, *Rutman 2006-0927-1*.

CP. Charlie Bell Well, *Monson 24 May 1957* (CAB). Childs Mt, 18 Aug 1992, *Felger 92-643B*.

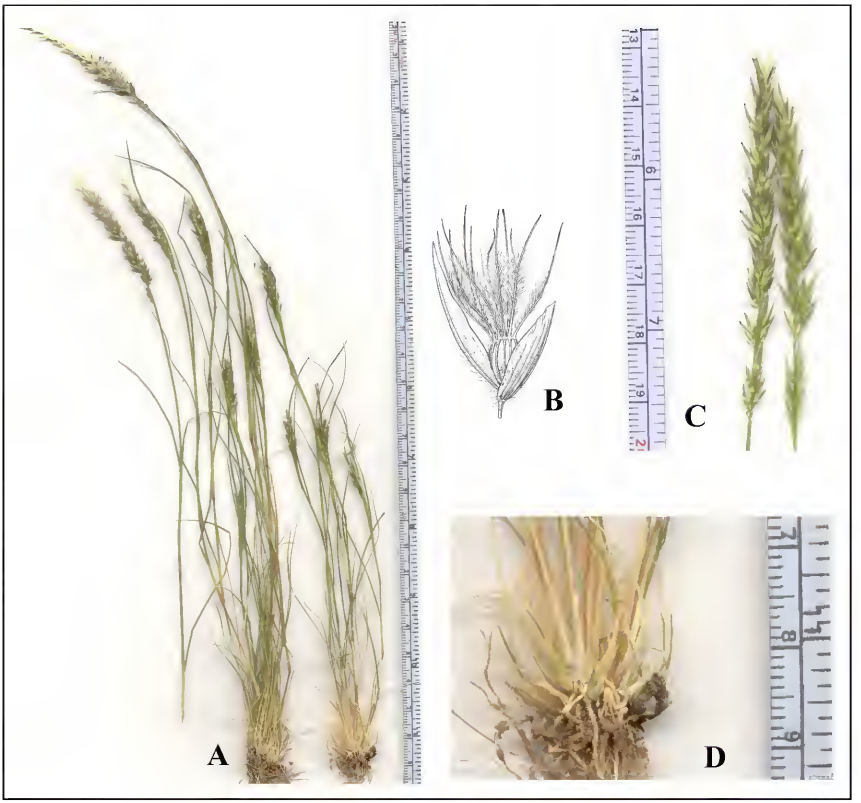

Figure 35. *Enneapogon desvauxii*. (A) Little Ajo Mts, Pima Co., 21 Sep 2008; (B) spikelet; (C) panicles, Alamo Canyon, 9 Sep 2013; (D) base of plant with cleistogenes, Little Ajo Mts, Pima Co., 21 Sep 2008.

Eragrostis – Lovegrass

Annuals/ephemerals or perennials, actively growing and reproductive during the warmer months, although some such as the Mediterranean *E. barrelieri* can be non-seasonal. Ligules ciliate with a line or band of hairs. Panicles with rebranching branches and usually overtopping the leaves, the branches and pedicels usually slender. Spikelets laterally compressed, with few–many florets, and awnless. Glumes thin; glumes and lemmas deciduous; lemmas 3-veined, the paleas often persistent. Anthers 3 (those in the flora area, elsewhere anthers 2 or 3).

1. Ephemerals, with prominent shining yellow, pink, or purplish glandular areas or rings at or below nodes, especially prominent on lower nodes of the panicles ..... **Eragrostis barrelieri**
1. Ephemerals or perennials, without large shining glandular areas or rings.

2. Hot weather ephemerals; anthers small, 0.3–0.4 mm long.

3. Panicles usually dense, the spikelets close together; pedicels usually shorter than mature spikelets; tiny, warty, glandular pits on culms, leaf margins, keels of glumes, lemmas, and lower leaf surfaces; spikelets 2–4 mm wide; grain 0.5–0.6 mm long..... **Eragrostis cilianensis**
3. Panicles usually open, spikelets usually widely spaced; pedicels longer or shorter than spikelets; without glandular pits; spikelets less than 2 mm wide; grain 0.6–0.8 mm long..... **Eragrostis pectinacea**

2. Perennials; anthers relatively large, 0.6–1.1 mm long.

4. Pedicels longer than the spikelets; spikelets 1.6–1.8 mm wide; anthers 0.6–0.8 mm long; grain conspicuously grooved on one side..... **Eragrostis intermedia**
4. Pedicels mostly shorter than the spikelets; spikelets 0.8–1.1 mm wide; anthers 1 mm long; grain without a groove..... **Eragrostis lehmanniana**

****Eragrostis barrelieri** Daveau
Mediterranean love grass

Small summer-fall ephemerals, often persisting through the winter or perhaps non-seasonal. The plants resemble those of *E. pectinacea* but are readily distinguished by shining yellow, pink, or purplish glandular areas or rings at or below the nodes and often especially prominent on lower nodes of inflorescences. These colored, glandular rings or patches are unique among Arizona grasses.

Known from the flora region from a single specimen at Lukeville and also observed in Sonoyta.

A weedy species native to southern Europe. The earliest Arizona record is from Tucson in 1918 and it was common in Tucson by the 1930.

Pima County: Lukeville, weed at U.S. Customs Station, 23 Oct 1987, *Felger 87-276*.

***Eragrostis cilianensis** (Allioni) Vignolo Lutati ex Janchen
Stink grass, stinking lovegrass; *zacate apestoso*. Figure 36.

Summer-fall ephemerals, highly variable in size, to 45 cm long but mostly much smaller. Plants with small crater-like glands, these turgid, viscous, and glistening when fresh. These glands are often used as a key character although they are sometimes scarce, especially on small plants, but if you look hard enough you will eventually find at least a few, which are small scale-like warts on margins and/or keels (midribs) of glumes, lemmas, and leaf blades and sheaths. Mouth of leaf sheaths bearded, the ligules ciliate. Spikelets 3.5–21 (26) mm × 2–3 (3.6) mm. Lemmas 2–2.5 mm long. Anthers 3 per floret, mostly 0.3–0.4 mm long. Grain 0.5–0.6 mm long, red-brown, broadly ovoid to subglobose and somewhat compressed laterally. The plants are usually recognizable in the field by the pale green (when fresh) or straw color (at maturity) of the relatively broad spikelets.

Common and widespread across the flora area in lowland habitats, mostly where water temporarily accumulates, wetland soils of dirt tanks, floodplains, swales, sandy washes, and adjacent desert flats during years of favorable summer rains.

Native to the Old World, now worldwide, often weedy; well established in the Sonoran Desert in disturbed as well as natural habitats. The common name refers to the strong odor of fresh plants growing in non-desert regions, such as moist temperate or subtropical regions where this grass is often relatively large and abundant. The plants lose the odor on drying. In the flora area and elsewhere in the Sonoran Desert it does not seem to live up to its common name, at least sometimes and according to some botanists.

OP: Sandy arroyos, N border of Monument, 11 Sep 1943, *Clark 10976* (ORPI [E of Armenta Ranch]). Ajo Loop Rd 2 mi NE of Visitor Center, 9 Sep 1984, *Van Devender 84-447*. 0.5 km E of Lukeville, 11 Nov 1987, *Felger 87-324*. Aguajita Wash, 14 Sep 1988, *Felger 88-436*. 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-6*.

CP: Dan Drift's Mine near Tule Well, *Simmons 3 Oct 1963* (CAB). Jose Juan Represo, 12 Jun 1992, *Felger 92-567*. 3.6 mi N of Christmas Pass, 27 Nov 2001, *Felger 01-535*. Tule Well, 27 Nov 2001, *Felger* (observation).

TA: Coyote Water, 25 Oct 2004, *Felger 04-21*.

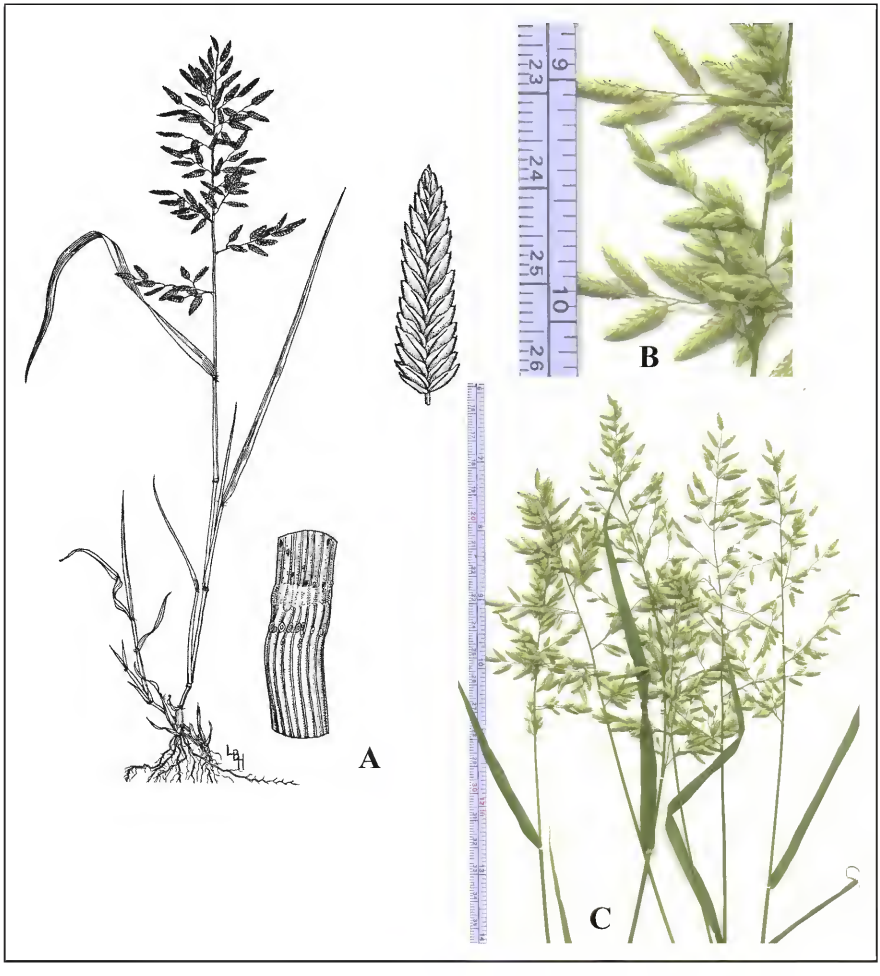

Figure 36. *Eragrostis cilianensis*. (A) Plant, portion of leaf sheath with glands, and spikelet; (B & C) panicles and spikelets, Why, Pima Co., 15 Sep 2013.

Eragrostis intermedia Hitchcock
Plains love grass. Figure 37.

Tufted perennials. Leaf blades mostly glabrous except densely hairy behind the ligule. Panicles 17–45 cm long, 10–30 cm wide, diffuse, and arching, with numerous slender, spreading branches. Pedicels very slender, slightly longer than the spikelets; spikelets 3–7 mm long, 1.6–1.8 mm wide, with 5–11 florets. Lemmas 1.8–2.2 mm long. Anthers three, 0.5–0.8 mm long. Grain 0.8–0.9 mm long, with a prominent groove.

Ajo Mountains, especially luxuriant at higher elevations and sometimes rooted in bedrock crevices, and locally in the Diablo Mountains.

Southern USA to South America.

Distinctions between *Eragrostis intermedia* and *E. lugens* Nees seem subjective and often become especially blurred in parts of Mexico. These involve overlapping sizes for spikelet width, lemma length, and supposed differences in the prominence of the caryopsis groove—*E. intermedia* is supposed to have a deeper groove (Gould & Moran 1981: 57; McVaugh 1983: 166–167; also see Peterson 2003: 97). John Reeder (pers. comm. to R. Felger, 2004) and Felger were not able to apply these features to separate these grasses. *Eragrostis lugens* was described in 1829 and has priority over *E. intermedia*, described in 1933.

OP: Ajo Mts, 31 Oct 11938, *Goodding 3720*. Alamo Canyon, *Nichol 4 May 1939*. Arch Canyon, 900 m, 2 Dec 1990, *Felger 90-561*. Bench Canyon, Ajo Mts, 3700 ft, *Henry 6 Nov 1978*. Bull Pasture Trail, 2800 ft, 20 Oct 1978, *Bowers 1544*. Diablo Mts, 807 m, shaded base of N-facing cliff, 22 Sep 2013, *Rutman 20030922-11*.

***Eragrostis lehmanniana** Nees
Lehmann love grass; *zacate africano*. Figure 38.

Tufted perennials (also flowering in the first year or season), sometimes with short stolons. Culms and panicles 50–60+ cm long, the culms usually bent at the lower nodes. Leaf blades 4–15 cm long. Panicles often 15–21 cm long, openly branched, the branches and pedicels ascending to spreading; pedicels usually less than ⅓ as long as the spikelets (or longer than spikelets on some terminal spikelets). Spikelets slightly compressed, often dark gray-green or straw colored, often 4–5.8 × 0.8–1.1 mm, with several–12 florets. Lemmas 1.7–1.8 mm long. Anthers 3 per floret, 1 mm long, conspicuously exserted and readily deciduous. Grain 0.6–0.8 mm long, ellipsoid with one side flattened.

This invasive grass is widespread and well established along roadsides and even natural areas to the north and east of the flora area and at the former military site and its access road on Childs Mountain. Highway 85 is the documented invasion route in Organ Pipe. In the late 1980s it was common at Why, north of Organ Pipe, but had not spread westward or southward into the drier and more natural desert areas. However, by the mid- to late-1990s it had spread southward along Highway 85 and became established on Bureau of Land Management lands near the northern boundary of the Monument. Since the mid-1990s occasional roadside plants have been found farther south along Hwy 85 within Organ Pipe and, since 2001, elsewhere in the Monument. In 2001 a population 10 meters long appeared along Hwy 85 at two miles north of the Visitor Center and scattered plants were found to the north. During this time Rutman actively removed these plants from the Monument. Suitable habitat exists in the Ajo Mountains where it could become a serious threat to the native ecosystem.

Figure 37. *Eragrostis intermedia* (A) Plant, panicle, and spikelet, (B) spikelets, Alamo Canyon, Ajo Mts, 12 Sep 2008, (C) young panicles, Arch Canyon, Ajo Mts, 14 Sep 2013

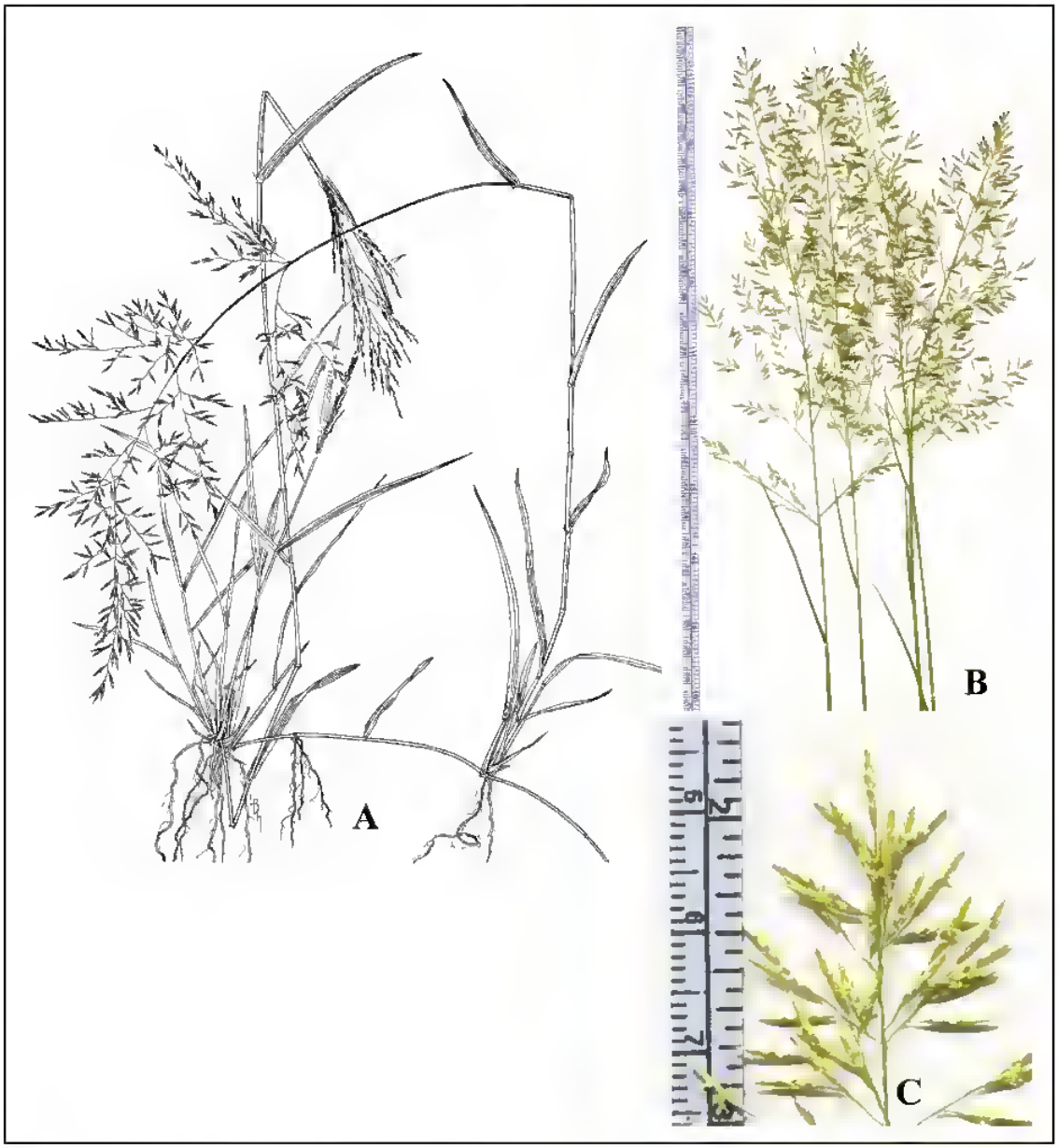

Figure 38. *Eragrostis lehmanniana*. (A) Plant with panicles Why, Pima Co.; (B) 15 Sep 2013; (C) 11 Sep 2008

Native to South Africa, introduced into Arizona by the U.S. Soil Conservation Service in the 1930s, and now well established in southern Arizona and much of northern Sonora as well as elsewhere in southwestern USA and northern Mexico.

OP: Gravel roadside, Hwy 85, 1 mi S of Visitor Center, single plant (removed), first ORPI record, *Rutman 9 May 1996* (ORPI). Planter at Visitor Center, *Rutman 14 Aug 2001* (ORPI). 7.9 mi W of Hwy 85 on S Puerto Blanco Drive, one plant (removed), *Rutman 27 Nov 2001* (ORPI).

CP: Childs Mt, 2300 ft, 18 Aug 1992, *Felger 92-647*.

Eragrostis pectinacea (Michaux) Nees var **pectinacea**
[*E. arida* Hitchcock, *E. diffusa* Buckley, E. *pectinacea* var. *miserrima* (E. Fournier) Reeder, *E. tephrosanthes* Schultes]
Carolina lovegrass. Figure 39.

Figure 39. *Eragrostis pectinacea*. (A) Las Playas, Cabeza Prieta, 28 Nov 2001, *Felger 01-560* (ASU, from SEINet); (B) spikelet, photo by Elizabeth Makings, from SEINet.

Delicate, filmy summer-fall ephemerals, and rarely growing with winter-spring rains or germinating in fall and persisting through the winter, (5) 12–60 cm tall. Panicles 7–20+ cm long, the branches and pedicels slender. Spikelets 2.6–5.5 × 1.2–1.4 mm; lemmas 1.4–1.8 mm long,

disarticulation begins with the glumes and then the lowermost florets (except the paleas) in sequence. Paleas translucent and tardily deciduous to persistent after lemmas and glumes have fallen. Anthers 3 per floret, 0.35 mm long, not exserted or barely so. Grain not grooved (immature grain sometimes folding inward upon drying).

Seasonally abundant in the large playas of Cabeza Prieta. There are no other modern records for this grass from the flora area although it is common in adjacent regions both north and south of the flora area (Felger 2000, 2007a). The fossil record shows this or a similar grass in two pinyon-juniper samples from the Ajo Mountains during the Pleistocene.

Eragrostis pectinacea var. *pectinacea* is one of the most widespread, hot-weather ephemeral grasses in southern Arizona and Sonora. It ranges from Canada to South America and the West Indies.

Three varieties are listed for the Americas. Variety *traceyi* occurs only in Florida. The other two, var. *miserrima* and var. *pectinacea*, are widespread including the Sonoran Desert Region and western North America (e.g., Felger 2000; Reeder 1986, 2012; also see SEINet). The distinctions are pedicels mostly appressed (var. *pectinacea*) or mostly spreading (var. *miserrima*)—the distinctions do not seem to be biologically significant. Plants identifiable to both varieties often grow intermixed in western North America, especially in the Southwest, and a single handful can give you plants identifiable to both varieties, or a single specimen may show features of both varieties (Figure 39A).

OP: †*E.* cf. *pectinacea*, Montezuma's Head, inflorescences fragments with attached paleas, 20,490 & 21,840 ybp.

CP: Las Playas, 28 Nov 2001, *Felger 01-560* (ARIZ, ASU, TEX, UC).

Eriochloa – Cup grass; *zacate taza*

The Sonoran Desert species are annuals growing during hot, wet, summer weather as weeds in well-watered places and in natural areas, especially in temporarily wet soils. They are among the first summer-fall grasses to shed their spikelets after maturity. The plants wither quickly with drying conditions at the end of summer and only a few weeks after the grain matures and falls there may be no sign of the plants. Culms relatively soft and sometimes semi-succulent. Ligules a line of soft hairs; leaf blades flat. Inflorescences panicles with spike-like branches. Spikelets panicoid, usually in pairs in two rows on one side of a slender rachis; spikelets teardrop shaped, quickly falling away when mature. The lower glume reduced and fused to a rounded callus derived from a segment of the rachilla to form a unique bulbous disk at the spikelet base. Fertile lemma firm and shiny, with conspicuous inrolled margins tightly gripping the palea and grain.

1. Spikelets 4–5 mm long from base of cup to awn tip ..... **Eriochloa acuminata**
1. Spikelets 6.5–8 mm long from base of cup to awn tip ..... **Eriochloa aristata**

***Eriochloa acuminata** (J. Presl) Kunth var. **acuminata**
[*E. lemmonii* Vasey & Scribner var. *gracilis* (E. Fournier) Gould]
Southwestern cupgrass; *zacate taza*. Figure 40.

Summer annuals often 30–50+ cm tall, the culms often weak. Leaf blades thin, flat, bright green, glabrous or sparsely hairy. Spikelets usually densely hairy, 4–5 mm long (including the cup and mucro). The glume awnless or extending into a short mucronate tip. Fertile lemmas awnless or with a mucronate tip to 0.1 (0.3) mm long.

Organ Pipe in temporarily moist soil in natural and disturbed habitats including areas adjacent to urban and agricultural areas in Sonoyta. The modern records indicate it has often spread in Organ

Pipe as a weed. It was, however, common in the Ajo and Puerto Blanco Mountains from about 1000 to 20,500 years ago. The florets are especially common in the Montezuma's Head middens, many of them complete with the basal cup and measuring to 5 mm long (including the awn).

Widespread in southwestern USA, both Baja California states, mainland Mexico and southwestern USA, from deserts to pine-oak woodland, and widely adventive elsewhere.

OP: 0.5 km W of Lukeville, 10 Nov 1987, *Felger 87-281*. 0.5 mi E of Lukeville, 11 Nov 1987, *Felger 87-314*. Residential area, common weed in lawn of *Cynodon dactylon*, 13 Sep 1986, *Felger 86-266*. Near N boundary 0.2–02 mi E of Hwy 85, artificial catchment created in 1940s, abundant, 21 Sep 2013, *Rutman 20130921-21*. †Montezuma's Head, florets, 13,500 & 20,490 ybp. †Puerto Blanco Mts, 980 ybp (Van Devender et al. 1990: 339).

Figure 40. *Eriochloa acuminata*. (A) Tributary of Cuerda de Lena, N boundary of Organ Pipe, 17 Sep 2013; (B) spikelets, Silver City, NM, 21 Oct 2007, Russell Kleinman, from Gilaflora.com.

Eriochloa aristata Vasey var. **aristata**
Bearded cupgrass; *zacate taza*

Similar to *E. acuminata* but generally more robust and with larger spikelets. Leaf blades glabrous or sparsely hairy. Spikelets 5.5–8 mm long from base of cup to the awn tip. The glume tapering to an awn 1.5–3 mm long. Fertile lemma with a stubby mucronate tip or awn point 0.15–0.4 mm long. Several early collections from Tucson have exceptionally long, slender spikelets (11–12 mm long).

Temporarily wet, muddy or sandy soils of dirt tanks, washes, and swales in the eastern part of Cabeza Prieta and at least the northern and west-central part of Organ Pipe. Perhaps more widespread with favorable summer-fall rains.

Eastward from Organ Pipe in southern Arizona. Southwestern USA to Central America and Columbia.

OP: Growler Canyon, 1.5 mi E of Bates Well Ranch, *Wirt 13 Oct 1988*. W of Hwy 85 on road to Armenta Ranch, 1 Feb 2002, *Felger 02-73a*. Grower Valley, 8 Oct 2006, *Rutman 20061008-4*
CP: Monreal Well, *Simmons, probably 20–21 Oct 1962* (CAB). Jose Juan Represo, 14 Sep 1992, *Felger 92-719*. Las Playas, 23 Sep 1993, *Harlan 411* (CAB).

Festuca – Fescue, ryegrasses
[*Vulpia*]

Small, winter-spring ephemerals (those in the flora area; elsewhere often perennials). Leaf sheaths usually open; ligules membranous; auricles none. Inflorescences usually of panicles, sometimes reduced, unbranched and racemose in drought-stressed plants. Spikelets laterally compressed, with multiple florets, the uppermost ones reduced. Glumes shorter than the lower lemmas, the lower glume shorter than the upper glume. Lemmas awned (those in the flora area).

About two dozen annual species worldwide have been segregated from *Festuca* as *Vulpia*. They tend to be small grasses with mostly cleistogamous flowers, usually with 1(2) stamen(s) and small stigmas. *Vulpia*, however, is not monophyletic and is nested within *Festuca* (e.g., Catalán et al. 2004). *Festuca* and *Poa*, each with about 500 species, are the largest genera of grasses and are worldwide in distribution. Except for the four ephemeral species in the flora area, these genera are essentially absent from the Sonoran Desert and there are relatively few species in deserts elsewhere.

1. Spikelets with 6 or more florets; awns mostly 5 (8) mm or less in length ..... **Festuca octoflora**
1. Spikelets with 5 or fewer florets; awns mostly 8–12 mm long ..... **Festuca microstachys**

Festuca microstachys Nuttall
[*F. grayi* (Abrams) Piper. *F. microstachys* var. *ciliata* A. Gray ex Beal. *F. microstachys* subsp. *grayi* Abrams. *F. microstachys* var. *pauciflora* Scribner ex Beal. *Vulpia microstachys* (Nuttall) Munro]
Small fescue

Small, slender ephemerals. Inflorescences of panicles 4–10 cm long, especially the lower branches spreading and often 1–3.5 cm long (excluding awns), or inflorescences unbranched and racemose. Axils of panicle branches and pedicels with a callus (seen with magnification and not visible on young plants where the branches and pedicels have not spread apart). Spikelets often 6–7 mm long (excluding awns), with 5 (rarely more) or fewer florets. Lower glumes much narrower and more than half as long as the upper glumes. Awns 9–12 mm long.

Ajo Mountains at least in Alamo Canyon and perhaps more common at higher elevations. It grew in the Tinajas Altas Mountains about 11,000 years ago.

Southern and central Arizona, mostly at elevations at or above the limits of the desert. Western North America from British Columbia to Baja California Sur. Not known for Sonora but expected in mountains in the northern part of the state.

Four varieties are sometimes recognized; var. *ciliata* occurs in the flora area. The varieties, however, are not geographically well marked—for example plants of var. *ciliata* with pubescent spikelets and var. *pauciflora* with glabrous or scabrous spikelets grow side by side in the Tucson Mountains.

OP. Slopes of Ajo Mts, *Albee Apr 1937*. Alamo Canyon, uncommon, among dense growth of spring annuals on N-facing bank of canyon bottom, intermixed with *F. octoflora*, *Poa bigelovii*, etc., 29 Mar 2003, *Felger 03-426*.

TA. †Tinajas Altas Mts, 10,950 ybp (Van Devender et al. 1990: 340).

Festuca octoflora Walter

[*Festuca octoflora* var. *glauca* (Nuttall) Fernald. *F. octoflora* var. *hirtella* (Piper) Henrard. *F. octoflora* var. *tenella* (Willdenow) Fernald. *Vulpia octoflora* (Walter) Rydberg. *Vulpia octoflora* var. *glauca* (Nuttall) Fernald. *V. octoflora* var. *hirtella* Piper. *V. octoflora* var. *tenella* (Willdenow) Fernald]

Six-weeks fescue, eight-flowered fescue. Figure 41.

Plants highly variable in size, 4–15 (29) cm tall, or as small as 2.5 cm with a single spikelet when severely drought-stressed. Culms mostly single or few, and with few small leaves above. Inflorescences of spike-like panicles, mostly 2–10 cm long, with mostly short and tightly appressed branches, or unbranched and racemose. Pedicels and small branches flattened below. Spikelets 8–13 mm long. Florets crowded, 6–13 (15) per spikelet. Lower glumes more than half as long as the upper glumes. Lemmas 4–8 mm long, tapering to a slender awn 1–8 mm long, the length generally uniform within a local population.

Widespread and seasonally common across the flora area; flats, washes, disturbed habitats, and rocky slopes including highest elevations in the Ajo Mountains. Substantially larger plants and higher densities occur in shaded as compared to unshaded sites. It has been in the region for at least 22,000 years.

One of the most common winter-spring ephemerals grasses in the Sonoran Desert. Across North America from Canada to northern Mexico, and introduced in Eurasia and South America.

Three varieties are often recognized, but like *Festuca microstachys*, they seem to be of doubtful biological significance (e.g., Arnow 1987; Lonard & Gould 1974; Holmgren & Holmgren 1977). Variety *hirtella* occurs in the flora area, characterized in part by scabrous or pubescent spikelets (lemmas). Plants in the flora area with glabrous or merely scabrous lemmas are probably immature plants of var. *hirtella* rather than var. *octoflora*.

OP. Alamo Canyon, *Nichol 14 Mar 1939*. 5 mi SW of Bates Wells Ranch, 12 Mar 1983, *Reeder 7583*. Quitobaquito, 29 Mar 1988, *Felger 88-116*. †Montezuma's Head, many florets with awns, 21,840 ybp.

CP. Charlie Bell Pass, 3 Apr 1992, *Whipple 3929* (CAB). San Cristobal Wash, 20 Mar 1992, *Harlan 31* (CAB). Agua Dulce Spring, 26 Feb 1993, *Felger 93-89*. Bassarisc Tank, 26 Feb 1993, *Felger 93-125*. Papago Well, 26 Feb 1993, *Felger 93-134*.

TA. Tinajas Altas, 1450 ft, *Van Devender 10 Mar 1980*. Coyote Water, 18 Mar 1998, *Felger* (observation). †Butler Mts, 11,250 ybp (Van Devender et al. 1990: 342). *V.* cf. *octoflora*. †Tinajas Altas Mts, 8970 to 10,950 ybp (4 samples, Van Devender et al. 1990: 340).

†**Festuca** (*Vulpia*) sp.

The small festucas (*Vulpia*) were important Ice Age grasses in the Ajo Mountains, especially about 20,000 years ago at Montezuma's Head. These fossils may be one or both species that occur in the region today.

OP: †Alamo Canyon, florets, 1150 to 32,000 ybp (3 samples). †Montezuma's Head, florets, 13,500 & 20,490 ybp.

Figure 41. *Festuca octoflora*. (A) Red Cone Campground, Pinacate Reserve, Sonora, 19 Mar 2010; (B) spikelets, photo by Elizabeth Makings, from SEINet.

Heteropogon contortus (Linnaeus) P. Beauvois ex Roemer & Schultes
[*Andropogon contortus* Linnaeus]
Tanglehead; *zacate colorado*. Figure 42.

Robust tufted perennials often 60–70 cm tall; culms erect, crowded. Dry leaves copper or rust-colored and persistent. Reproductive primarily during warmer months. Inflorescences of

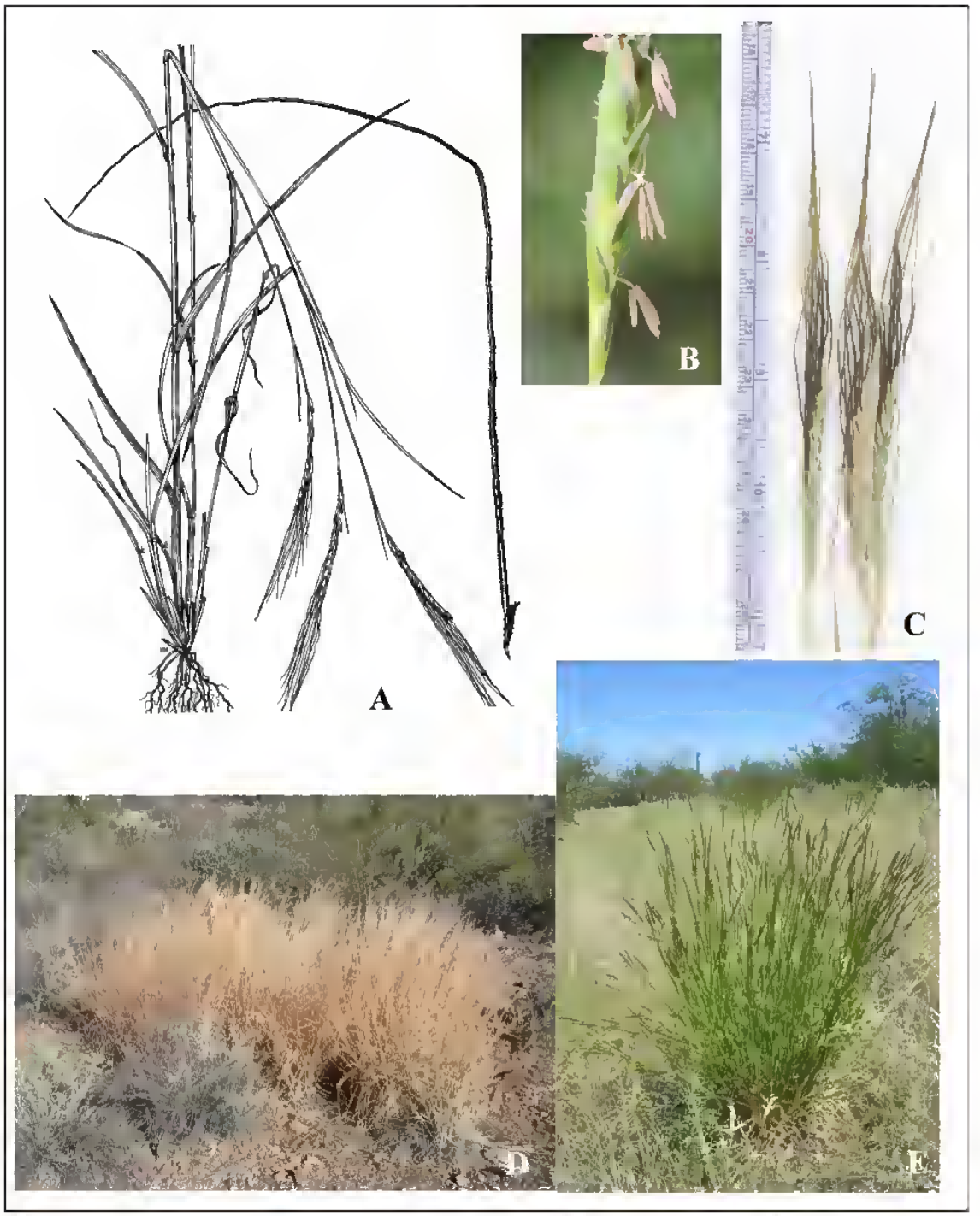

Figure 42. *Heteropogon contortus*. (A) Plant and fertile floret with its large awn, (B) portion of young rame with exserted anthers, Diablo Mts, 12 Sep 2013; (C) three rames, Chuckwalla Hills, Organ Pipe, 6 Oct 2013; (D) copper-colored dormant plants, Arch Canyon, Ajo Mts, 27 Dec 2007, (E) roadside, Hwy 85 south of Why, Pima Co., 25 Sep 2004

unilateral rames (note that the awns are all on one side), one per culm or branch, breaking apart at maturity. Spikelets andropogonoid, in pairs very different from each other (a few spikelet pairs at

lower nodes of inflorescences may be staminate and sessile). (1) Pedicelled spikelets awnless and sterile, the lower glume 7–10 mm long (not including the short pedicel), green when fresh (the larger of the two glumes, and generally the only one you can see without dissecting the spikelet), glabrous or with a few bulbous-based large hairs; pedicelled spikelets larger than the body of the sessile spikelets. (2) Sessile spikelets bisexual, bearing a stout awn 4.5–7+ cm long, twisted and twice bent when mature, tawny brown with a needle-sharp base that "readily penetrates clothing and is a ferociously efficient dispersal mechanism" (Clayton & Renvoize 1986: 359).

Arroyos, larger washes, canyon bottoms, near waterholes, and hills and mountain slopes sometimes to their peaks; widely scattered and usually localized across the flora area. It has been at Tinajas Altas for at least 8000 years. East of Organ Pipe, on the Tohono O'odham Reservation, this native grass has been observed out-competing and gradually displacing the invasive *Eragrostis lehmanniana*.

Southwestern USA to South America and warm regions of the Old World. Although some authors have claimed it is "adventive in America since the time of Columbus" (Correll & Johnston 1970: 201; also Barkworth 2003), it has been in southwestern North America at least since the last Ice Age (e.g., Felger 2000; Felger et al. 2012; Van Devender et al. 1990).

OP. Quitobaquito, 30 Jan 1894, *Mearns 2752*. Alamo Canyon, *Nichol 4 May 1939*. Bull Pasture trail, 20 Oct 1978, *Bowers 1545*. Mouth of Estes Canyon, 17 Sep 1992, *Reeder 8911*. Diablo Mts, wash, along Ajo Mt Drive, 12 Sep 2013, *Rutman 20130912-6*.

CP. Tule Mts, 11 Feb 1894, *Mearns 2803* (US). S end of Cabeza Prieta Mountains, 1200 ft, 29 Feb 1976, *Fugate 694*. Little Tule Well, 18 Aug 1992, *Felger 92-651*. 3.4 mi N of Tule Tank, 2 Feb 1992, *Felger 92-71*. Sierra Pinta, summit, *Cain 15 Nov 2003*. Observations Cabeza Prieta Tanks, Heart Tank, North Pinta Tank, 14 & 15 Jun 1992, *Felger*; Daniels Arroyo at Charlie Bell Rd, 25 Feb 1993, *Felger*.

TA. Tinajas Altas Mts, 1200 ft, *Van Devender 25 Mar 1983*. †Tinajas Altas Mts, 5860 to 7860 ybp (Van Devender et al. 1990: 341).

Hilaria – Galleta

Perennials, growth and flowering response primarily during the warmer months. Leaves usually relatively short. Inflorescences slender and spike-like panicles with very reduced branches, the main axis zigzag and remaining after the spikelets fall. Spikelets in clusters of 3 at each node of the zigzag rachis, the clusters falling as a unit; central spikelet with 1 floret and bisexual or female, differing in form from the two lateral spikelets, the lateral spikelets each with 2 male or sterile flowers. All glumes together forming a false involucre. Lemmas 3-veined, awned or awnless.

Among the ten species of *Hilaria*, three sister species are sometimes segregated as *Pleuraphis* or else treated as subgenus *Pleuraphis*.

1. Plants mostly less than 30 cm tall, with slender stolons; culms glabrous ..... **Hilaria belangeri**
1. Plants mostly more than 40 cm tall, with strong, short rhizomes and lacking stolons; culms with felt-like or fine woolly hairs, at least near the base of the plant (older stems and leaf sheaths may become glabrous with age) ..... **Hilaria rigida**

Hilaria belangeri (Steudel) Nash
[*H. belangeri* var. *longifolia* (Vasey) Hitchcock]
Curly mesquite; *zacate chino*

Small, tufted perennials, mostly less than 15 cm tall, some to 28 cm; with long, slender, stolons (above-ground stems); culms slender, glabrous or with hairs at nodes. Leaf blades relatively

short, often curling, and with bulbous-based hairs. Growing and reproductive during warmer months. Inflorescences slender, 2–5.5 cm long with 4–10 (14) spikelet clusters, the spikelet clusters 4.5–7 mm long with sparse pubescence basally of hairs 0.1–0.4 mm long. Glumes conspicuously fused basally and with slender awns 2.5–5 mm long.

Ajo and Diablo Mountains; forming scattered, small to large patches, often on slopes, and covering an extensive area in Bull Pasture in the Ajo Mountains.

Widespread in Arizona, mostly above and at the upper margins of the deserts. Also Texas, Baja California Sur, and Sonora to Tamaulipas and south-central Mexico.

OP. Ajo Mt Drive 6.7 mi by road N [NE] of Visitor Center [Diablo Mts], 5 Nov 1977, *Bowers 924* (ORPI). Bull Pasture: 9 Apr 2005, *Felger 05-179*, Shallow sediments in bedrock pockets, 18 Mar 2005, *Rutman 20050318-10* (ORPI).

Hilaria rigida (Thurber) Bentham ex Scribner
[*Pleuraphis rigida* Thurber]
Big galleta; *tobosa*. Figure 43.

Large tufted or bushy perennials forming dense clumps, often 0.5–1.2 m tall, the bases tough and knotty with short, almost woody rhizomes; roots tough and wiry. Culms rigid and stout, with felt-like white hairs, these readily rubbing off. Leaf sheaths glabrous; blades spreading, (4) 7–23 cm long, the length apparently depending upon soil moisture, the shorter blades commonly firm and sharp-tipped. Growth and flowering response especially during the warmer months, but some flowering may occur at least from February to November; plants becoming dormant or with considerable dieback during extended drought. Inflorescences densely flowered, (4.5) 5–13 cm long, the zigzag main axis remaining long after the spikelet clusters fall; sometimes forming a large, swollen gall structure 5–6 × 2–3 cm in place of an inflorescence. Spikelet clusters overlapping, each with a dense basal tuft of white hair. Spikelets (excluding awns) 6–10 mm long, fringed on their blunt tips. Glumes not obviously fused below, slender, lanceolate to narrowly oblong. Glumes, lemmas, and paleas more or less equal in length. Number and size of awns varying with position of spikelets and from one cluster to the next; glumes and lemmas each with (3 or 4) 5–7 veins, all, some, or none extending into awns 0.7–7 mm long. Lemma margins densely ciliate with silky hairs. Stigmas lavender to bluish purple. Spikelets often tinged pink to purple-brown during cool, dry seasons; usually drying straw-colored with prominent veins.

Common and widespread in Organ Pipe and increasingly abundant westward in Cabeza Prieta and the Tinajas Altas Region. Mostly on valley plains, sand flats, and dunes, although sometimes locally common on rocky slopes. Big galleta, bush muhly (*Muhlenbergia porteri*), and bamboo muhly (*M. porteri*) are the only shrubby grasses in the region. Big galleta, along with creosotebush (*Larrea*), is one of the most persistent and drought resistant perennials in the region. However, Rutman observed that the severe drought of the 2000s caused extensive dieback of *H. rigida* in the flora area, and a significant percentage of plants died. Rhizomes can survive and resprout after a low-temperature fire. This grass has been in the western margin of the flora area for more than 10,000 years.

Western Arizona, southwestern Utah, southern Nevada, southeastern California, northwestern Sonora, and northeastern Baja California.

OP. Bates Well, *Nichol 26 Apr 1939*. 2 mi NW of Visitor Center, 8 Mar 1987, *Van Devender 87-8*. E of Armenta, *Wirt 8 Aug 1988* (ORPI). Quitobaquito, 14 Sep 1988, *Felger 88-466*.
CP. Charlie Bell Pass, 3 Apr 1992, *Whipple 3931* (CAB). San Cristobal Wash, 20 Mar 1992, *Harlan 24* (CAB). Pinta Sands, 11 Apr 1993, *Felger 93-405*.

TA: Coyote Water, 25 Oct 2004, *Felger 04-46*. Tinajas Altas, above the tinajas, 19 Mar 1998, *Felger* (observation) Surveyors Canyon, 29 Mar 2010, *Felger 10-201* †Butler Mts, 3820 to 10,400 ybp (3 samples, Van Devender et al 1990: 342)

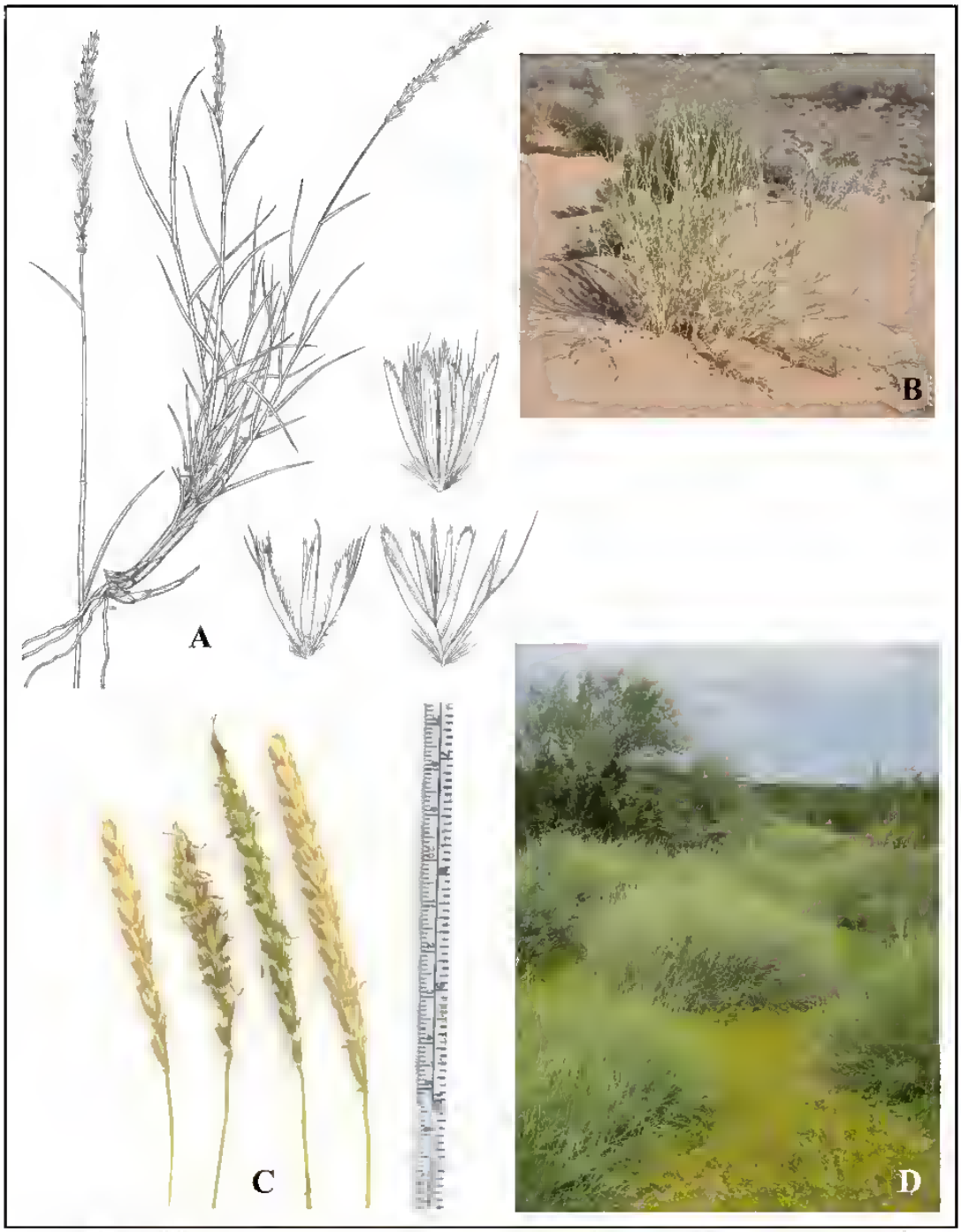

Figure 43. *Hilaria rigida*. (A) Plant and inflorescence, and spikelets: bisexual spikelet lower left, staminate spikelets lower right, and spikelet cluster upper right, (B) dunes SW of Las Playas, Gran Desierto Biosphere Reserve, Sonora, 28 Mar 2013; (C) panicles, Why, Pima Co., 31 Mar 2013; (D) N of Pozo Nuevo, Organ Pipe, 16 Aug 2012.

Hopia obtusa (Kunth) Zuloaga & Morrone
[*Panicum obtusum* Kunth]
Vine mesquite, *zacate de guia*. Figure 44.

Figure 44. *Hopia obtusa*. (A) Plant and spikelet, with fertile lemma and palea spread open. Bull Pasture. (B & C) 25 Sep 2013, (D) 24 Sep 2006, (E) stolons and young shoots, 25 Sep 2013.

Perennials to about 50 cm tall, with hard, knotty bases and long, slender stolons sometimes to 1 m or more in length with swollen and conspicuously hairy (villous) nodes. Culms tough, slender, mostly erect and with swollen nodes. Inflorescences of slender panicles with appressed unilateral branches. Spikelets panicoid, usually crowded, paired, 2.8–4 mm long, firm, blunt-tipped, bead-like, and brown when mature; with a staminate lower floret and a bisexual upper floret. Glumes about ¾ as long as the spikelet. Lower floret staminate with a lemma similar to the upper glume and a well-developed palea. Fertile lemma firm, smooth and shiny with inrolled margins tightly clasping the palea and enclosed grain. Stigmas maroon; anthers bluish purple. Reproductive during warmer months.

Ajo Mountains at least at Bull Pasture and one record at the north end of the Monument.

Generally above the desert in Arizona and Sonora. Southeastern and midwestern USA to central Mexico.

OP: Bull Pasture, moist soil near streambed, 9 Aug 1979, *Bowers 1796*. Armenta Ranch, ditch along road, *Rutman 4 Oct 1995* (ORPI). Ajo Mountains, 3100 ft, common, growing with *Pappophorum vaginatum* at junction of Bull Pasture Trail and seasonally wet stream in Bull Pasture, 24 Sep 2006, *Rutman 20060924-3*.

Hordeum – Barley, *cebadilla*

Winter-spring ephemerals (those in the flora area). Inflorescences terminal, unbranched, breaking apart at maturity and often called a "spicate raceme." Spikelets in triplets per node, relatively large, bearing long, scabrous awns, with one central, sessile spikelet and two, lateral pedicelled spikelets; spikelets, with 1 floret, glumes narrowed into firm bristles or awns. Central spikelet fertile (bisexual), the rachilla extended into a bristle behind the palea, the glumes side by side, bristle-like or somewhat flat in the basal part and in front of and often partially obscuring the fertile spikelet, the lemmas ovate, sharp-pointed, and essentially awnless or awned with a long, stout bristle. Lateral spikelets usually short-stalked, staminate or sterile (or fertile in most cultivated barleys), usually smaller than the central spikelet, often represented only by 3 awns or bristles. The triplet clusters alternate in cavities of the rachis in 2 longitudinal rows in wild and weedy species (often in 4 or 6 rows in cultivated barleys). In wild and weedy barleys the triplet clusters fall as a unit with the stalk-like rachis joint; in cultivated barleys the rachis is continuous and non-shattering.

1. Auricles present (ear-like or tongue-like flaps on each side of summit of leaf sheath); spikes 10+ mm wide (excluding awns); glumes of central spikelet long-ciliate on both margins; larger awns more than 15 mm long ..... **Hordeum murinum**
1. Auricles absent; spikes 4–8 mm wide (excluding awns); glumes not ciliate; awns 7–12 mm long ..... **Hordeum pusillum**

***Hordeum murinum** Linnaeus subsp. **glaucum** (Steudel) Tzvelev
[*H. leporinum* Link subsp. *glaucum* (Steudel) T.A. Booth & A.J. Richards. *H. stebbinsii* Covas]
Wild barley; *cebadilla silvestre*. Figure 45.

Plants variable, to 60 cm tall. Leaf auricles to 8 mm long. Inflorescences linear-oblong, 5.5–9.5 cm long (including awns), sometimes maturing partially enclosed by the uppermost leaf sheaths. Lateral spikelets with one of the glumes bearing long, spreading cilia on the margins, the other glume scabrous. Both glumes of the central spikelet are ciliate-margined, slightly flattened at their bases, and extend into a bristle. Stamens included within the florets, persistent and not exserted (enclosed or hidden by the lemmas and paleas); anthers of the central spikelet 0.5 mm or less in length and purple-spotted, those of lateral spikelets often 1+ mm long.

Well established along major washes in the eastern part of the Cabeza Prieta and scattered populations in Organ Pipe along roadsides, washes, and canyons. Extending into southeastern Organ Pipe from adjacent Sonora, where it is a common weed in disturbed habitats. It can form extensive stands in favorable habitats. It was at Quitobaquito in 1939 but has not been found there since.

Native to the Mediterranean and Middle East, now widespread and weedy in temperate regions of the world including western North America.

The mature inflorescences "may cause mechanical injury, when ripe, to nose and mouth membranes of grazing animals. The sharp-pointed rachis and rachilla joints and stiff awns of the mature spikelets are capable of penetrating both skin and flesh" (Gould 1951: 105–106). Dogs are also susceptible to this form of injury.

OP: Quitobaquito, *Nichol 28 Apr 1939*. Growler Canyon, 30 Mar 1979, *Bowers 1606*. Gachado Line Camp, 11 Nov 1987, *Felger 87-327*. Alamo Canyon, corrals at abandoned ranch, 29 Mar 2003, *Felger 03-398*.
CP: San Cristobal Wash, 20 Mar 1992, *Harlan 33* (CAB). Daniels Arroyo at Charlie Bell Road, 25 Feb 1993, *Felger 93-72*.

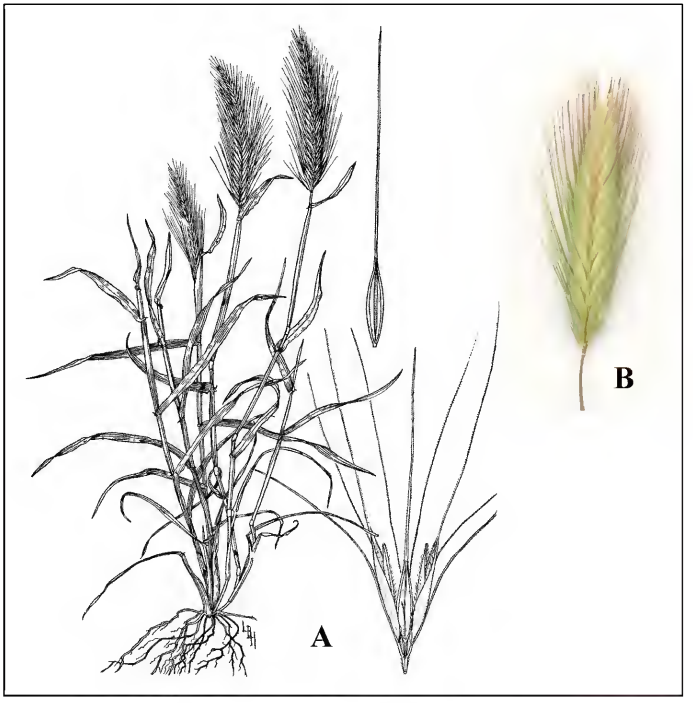

Figure 45. *Hordeum murinum*. (A) Plant, spikelet triplet, and floret with long bristle; (B) spikelet, Tucson, 2 Apr 2008.

††**Hordeum pusillum** Nuttall
Little barley

The plants including the inflorescences are generally smaller than those of *H. murinum*, without leaf auricles, and the inflorescences more slender and compact.

It was in the Ajo and Puerto Blanco Mountains at least from 8000 to 20,500 years ago. The nearest known, present-day population occurs at higher elevations in the Sand Tank Mountains. It should be sought at higher elevation in the Ajo Mountains.

Widespread in Arizona, but not in the lowland desert of the southwestern part of the state, and one record in north-central Sonora. Canada to northern Mexico.

OP: †Montezuma's Head, florets, 20,490 ybp. †Puerto Blanco Mts, 7970 ybp (Van Devender et al. 1990, 339).

Leptochloa – Sprangletop

As previously constituted, this familiar genus has been shown to be polyphyletic (Peterson et al. 2012), and those in the flora area distributed among three genera, with *Trichloris crinita* transferred to *Leptochloa*.

Leptochloa dubia, see **Disakisperma dubia**
Leptochloa fusca subsp. *uninervia*, see **Diplachne fusca** subsp. **uninervia**
Leptochloa panicea subsp. *brachiata*, see **Dinebra panicea** subsp. **brachiata**
Leptochloa viscida, see **Dinebra viscida**

Leptochloa crinita (Lagasca) P.M. Peterson & N. Snow
[*Chloris crinita* Lagasca. *Trichloris crinita* (Lagasca) Parodi. *T. mendocina* (Philippe) Kurtz]
Feather fingergrass; *zacate escoba*. Figure 46.

Robust tufted perennials; tallest ones along the southern border of Organ Pipe often reach 1–1.2+ m tall, some growing through desert shrubs, elsewhere in Organ Pipe generally less than 0.5 m tall; sometimes flowering in first season or year. Growing and reproductive primarily during the warmer months. Plants sometimes producing rhizomes. Culms upright and firm. Inflorescences panicles of mostly 6–20 erect, bristly white spicate branches 9–15 cm long clustered at the top of the culm. Spikelets crowded, with 1 fertile and 1 sterile floret (occasionally 2 in other regions), each with 3-veined lemmas, the veins extending into 3 slender awns often 1.5–2 cm long; sterile floret cylindrical, similar to the fertile floret but much smaller.

Localized on alkaline soils among low hills in the southern margin of Organ Pipe west and east of Lukeville and locally in the Ajo and Puerto Blanco Mountains.

Arizona to western Texas, south to Durango, Coahuila, Sonora, and Baja California Sur and in South America.

OP: W side of Alamo Canyon, 13 Sep 1941, *Goodding 307-41*. Boulder Canyon, 3 May 1978, *Bowers 1290* (ORPI). 0.5 km W of Lukeville [Dowling Ranch area], 10 Nov 1987, *Felger 87-280* [ca. 90 cm tall]. 4.5 km E of Lukeville, 15–20 m N of border fence, well established colony, but much more common on the Sonoran side of the fence, 11 Nov 1987, *Felger 87-330*. Puerto Blanco Drive, 9.3 mi W of Hwy 85, 14 Sep 1988, *Felger 88-400*. Puerto Blanco Mts, small tributary to Cherioni Wash near Red Tanks trailhead, 21 Sep 2013, *Rutman 20130921-8*.

Figure 46. *Leptochloa crinita*. (A) Plant, panicle, and spikelet with glumes separated (from Hitchcock 1951); (B) panicle, near Red Tanks parking area, North Puerto Blanco Drive, Puerto Blanco Mts, 20 Sep 2013.

Melica frutescens Scribner
Bushy melic, woody melic

Coarse, tufted perennials to 90 cm tall (to more than 1 m tall elsewhere), with brittle stems and purple dye at culm bases and sometimes in leaf sheaths and ligules. Leaf sheaths closed nearly to the top; ligules thin and membranous; leaf blades 10–17.5 cm long. Inflorescences panicles 6–12 cm long, robust and slender, with slender, appressed branches, and erect, appressed spikelets. Spikelets silvery-papery, 9–18 mm long, awnless, breaking apart below the glumes and readily falling entire, with 3–5 bisexual florets and terminal vestigial florets (rudiments) 2–6 mm long resembling the bisexual florets in shape; glumes 7–15 mm long, lower lemmas ca. 10 mm long. Grain shiny, free from the lemma and palea, and longitudinally furrowed. Reproductive at least March to early May.

Ajo Mountains, mostly at higher elevations, and sometimes descending into larger canyons. This isolated population is poorly known.

In Arizona otherwise known from the Tonto National Forest and the Estrella and Superstition Mountains in Maricopa County. Widespread, especially in non-desert areas, of California, Baja California, and northern Baja California Sur.

OP: Alamo Canyon, 13 Sep 1941, *Goodding 302-41*. Arch Canyon, 2600–3200 ft, 3 May 1978, *Bowers 1300*

Muhlenbergia – Muhly grass

Annuals/ephemerals and perennials of diverse growth forms and sizes. Ligules membranous and not ciliate. Inflorescences of highly diverse panicles. Spikelets small, with 1 floret, breaking off above the glumes. Lemmas firm, slender, 3-veined, 1-awned or awnless. Grain usually slender, fusiform, not readily falling from the floret; pericarp closely covering the seed. Key characters include membranous ligules, spikelets with 1 floret, and 3-veined lemmas.

This is the most taxonomically diverse genus of grass in the flora region and includes nine species. *Muhlenbergia microsperma* is the only member of the genus ranging across the entire flora area, including the more arid regions. *Muhlenbergia porteri* occurs in some lowland desert areas, while the remaining muhly grasses are essentially non-desert species and in the flora area are known only from the Ajo and Diablo Mountains.

Muhlenbergia is one of the most taxonomically diverse genera in southwestern North America. This genus includes more than 160 species, mostly in the Western Hemisphere.

1. Delicate ephemerals; root systems often weakly developed (except *M. tenuifolia*).

2. Spikelets awnless ..... **Muhlenbergia fragilis**
2. Spikelets awned.

3. Plants not forming cleistogenes; glumes acute to acuminate ..... **Muhlenbergia tenuifolia**
3. Lower leaf axils bearing cleistogenes, these narrowly conical, awnless and without glumes, 4–10 (12) mm long; glumes of awned florets obtuse to somewhat acute.

4. Panicles conspicuously contracted (branches close together); glumes 1–2 mm long, the body of the lemma 4–6.2+ mm long ..... **Muhlenbergia appressa**
4. Panicles loose, open and feathery; glumes 0.5–1.3 mm long, the body of the lemma 1.8–2.5 (3) mm long ..... **Muhlenbergia microsperma**

1. Perennials; root systems well developed from a hard, knotty base.

5. Plants resembling a miniature bamboo, often more than 1 m tall, the culms woody below, branched above ..... **Muhlenbergia dumosa**
5. Plants not bamboo-like, generally not more than 1 m tall, culms not woody and not branched above (except *M. porteri*).

6. Plants bushy, not tufted, the stems slender, and profusely branching above; panicles often as wide as long, and open with spreading branchlets ..... **Muhlenbergia porteri**
6. Plants tufted, not bushy, not profusely branched above; panicles longer than wide, contracted or at least the branches ascending, appressed, or not evident.

7. Spikelets in pairs, one usually staminate or sterile and the other bisexual; lower glume with (1) 2 or 3 awns 0.5–4+ mm long ..... **Muhlenbergia phleoides**
7. Spikelets alike and not in pairs; glumes unawned or occasionally with 1 awn to 0.5 mm.

8. Plants delicate, 25–55 cm tall (or long), the culms slender; panicles 8–12 (20?) cm long..... **Muhlenbergia tenuifolia**
8. Plants robust, mostly 50–100 cm tall, the culm not especially slender; panicles (9) 20–40 cm long.

9. Panicles more than 3 cm wide (often contracted when young); spikelets awned, the lemmas awns to 15+ mm long ..... **Muhlenbergia emersleyi**
9. Panicles less than 1 cm wide; spikelets awnless or sometimes with a thick awn to 1.2 mm long ..... **Muhlenbergia rigens**

Muhlenbergia appressa C.O. Goodding
Devil's Canyon muhly. Figure 47.

Small, delicate ephemerals, apparently non-seasonal although mostly documented during the cooler seasons, sometimes reaching 40 cm tall but usually much smaller. Cleistogenes form in the lower leaf nodes. Panicles markedly contracted. Spikelets 4–7 mm long (not including the awn); glumes 1–2 mm long, the lemma slender, terete, with an awn 10–30 mm long. Reproductive with spring and summer-fall rains.

Ajo Mountains, recorded along Alamo Canyon and common in shady microsites, especially in upper elevations.

Central and southern Arizona, generally above the desert. Also southern California and both states of Baja California; not known but predicted for northern Sonora.

The plants of *Muhlenbergia appressa* generally resemble those of *M. microsperma* in habit and their similar-looking cleistogenes. Although they are clearly distinct, they are apparently closely related and are the only members of the genus in the flora area normally to have cleistogenes (Clayton & Renvoize 1986; Peterson & Annable 1991).

OP. Alamo Canyon *Nichol 4 May 1939*, Soil in bed of canyon, 17 Dec 1945, *Goodding 472-45*. Middle fork Alamo Canyon near crestline of Ajo Mts, 15 Mar 2003, *Rutman 2003-339*.

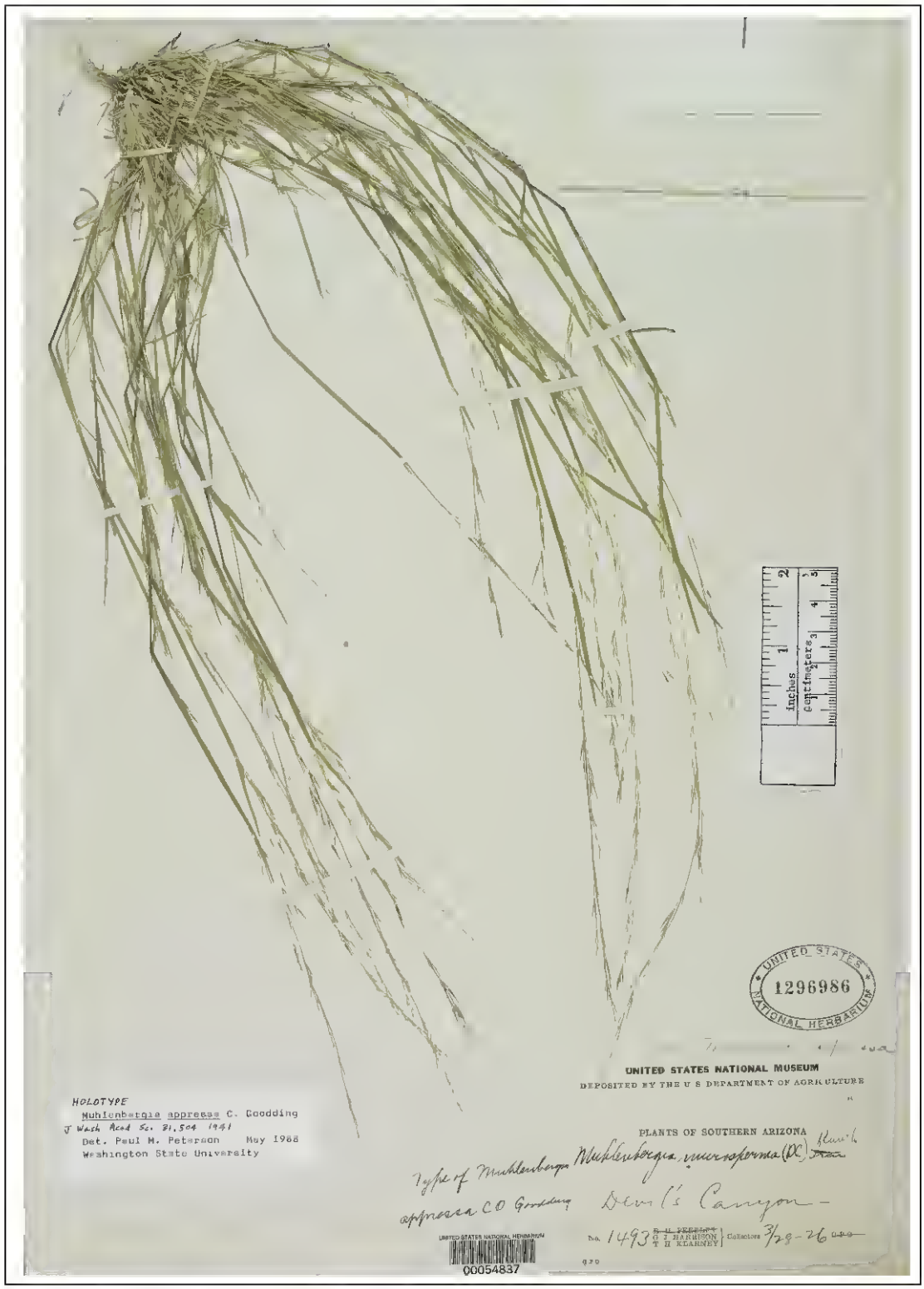

Figure 47. *Muhlenbergia appressa*. Devil's Canyon, Pinal Co., 28 Mar 1926, *Harrison & Kearney 1493* (holotype, US).

Muhlenbergia dumosa Scribner ex Vasey
Bamboo muhly; *carricillo*, *otatillo*. Figure 48.

Perennials, the larger plants often 1–1.5 (2+) m tall with slender, bamboo-like culms, woody at the base, the much-branched above, and with short, thick rhizomes, often forming clonal colonies. Upper branches filmy with numerous slender leaves. Panicles slender and densely flowered, usually held above the leaves, about 3 cm or less in length, the spikelets 2.5–3 mm long with awns to 8 mm long but mostly much shorter, or some spikelets awnless. Reproductive late February to early April.

Ajo and Diablo Mountains, locally common in canyons, at cliff bases, and on north-facing slopes and ledges to the crestline, often in shaded places.

Widespread in southern Arizona, mostly at elevations near the upper limits of the desert. Also Baja California Sur, Sonora to Jalisco, and the Chihuahuan Desert Region.

The fruits are often infected with a smut fungus, *Ustilago muhlenbergiae* Henning (identified by Robert L. Gilbertson, 2001). The only other smut reported for this grass is *U. sonoriana* Zundel, on plants from near Bavispe, Sonora (Fischer 1953). *Ustilago muhlenbergiae* is also known in southern Arizona from *Muhlenbergia pauciflora*, *M. porteri*, and *M. texana* (Rhodes & Gilbertson 1972).

OP. Alamo Canyon, 2500 ft, *Nichol 14 Mar 1939*. Arch Canyon, 17 Sep 1982, *Reeder 8909* (fruits with smut), 3300 ft, *Tinkham 19 Apr 1942* (fruits with smut). Bull Pasture Trail, *Bezy 25 Oct 1964* (fruits with smut). W slope of Montezuma's Head, above Pitahaya Canyon, 16 Jan 1976, *Van Devender 76-3* (fruits with smut). Diablo Mts, 807 m, shaded base of N-facing cliff, large clone/plant at shaded base of N-facing cliff, 22 Sep 2013, *Rutman 20130922-18*.

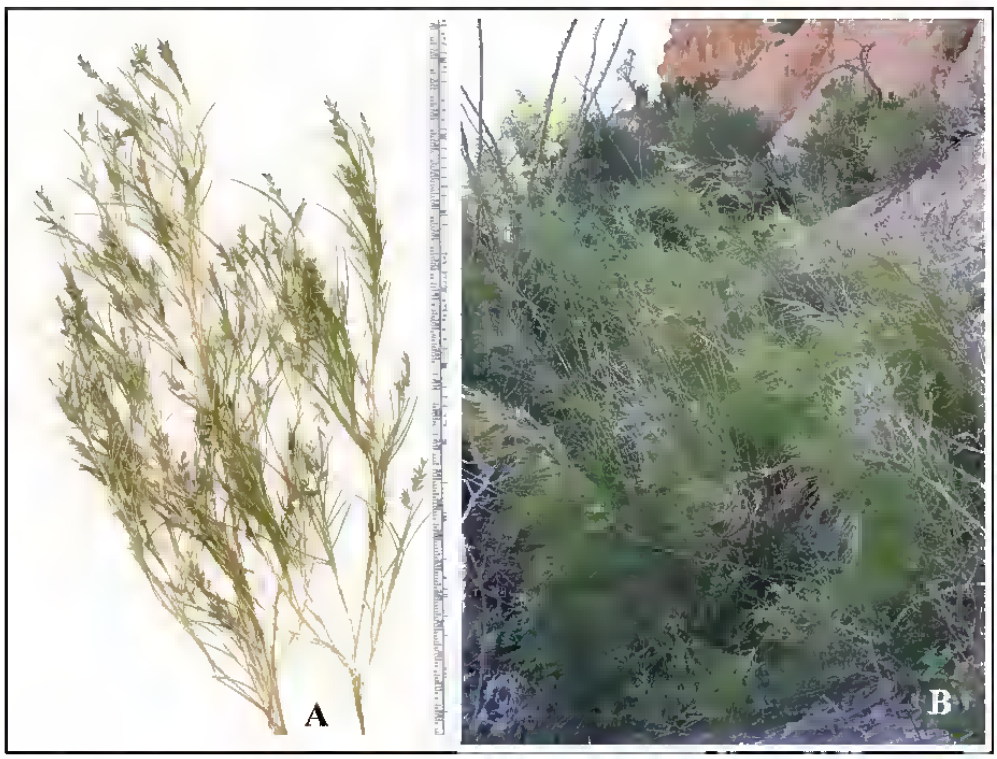

Figure 48. *Muhlenbergia dumosa*. (A) Arch Canyon, Ajo Mts, 31 Mar 2008, (B) trail to Bull Pasture, 24 Sep 2006.

Muhlenbergia emersleyi Vasey
[*M. gooddingii* Soderstrom]
Bullgrass, bull muhly, *zacate de toro* Figure 49

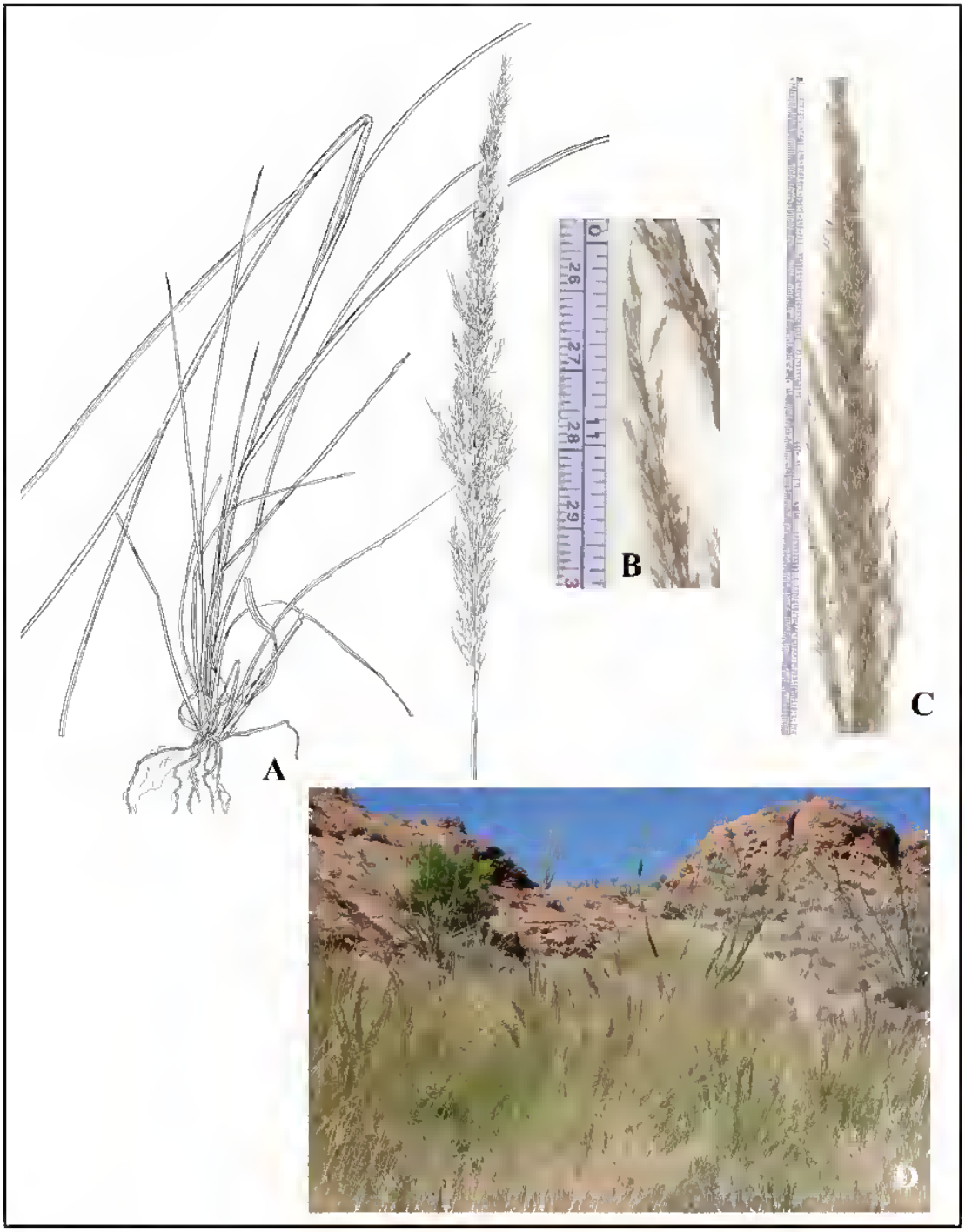

Figure 49 *Muhlenbergia emersleyi* (A) Plant and a panicle, (B &C) portion of panicle, Dragoon Mts, East Cochise Stronghold, 13 Oct 2013; (D) saddle between Arch & Boulder canyons, Ajo Mts, 21 Sep 2008.

Robust tufted perennials, often 0.5–1 m tall. Leaf sheaths compressed and conspicuously keeled (in cross section) near the base. Panicles large and feathery, 20–40 cm long, the branches ascending and densely flowered. Spikelets 2–3 mm long not including the awn; glumes about as long as, or slightly exceeding, the florets; lemma midrib extending in an awn to 1.5+ cm long and mostly deciduous, or sometimes awnless.

Ajo Mountains, common at upper elevations. *Muhlenbergia emersleyi* has a 22,000-year history in the Ajo Mountains.

Widespread in Arizona above the desert. Also Nevada to Texas, and well represented in non-desert regions of northern Mexico and southward to Durango and Oaxaca.

OP: Ajo Mountains, 1 Nov 1938, *Goodding M-373*. Bench Canyon, 3600 ft, *Henry* 6 Nov 1977 (ORPI). Bull Pasture Trail, 3000 ft, with *Vauquelinia californica* and *Quercus ajoensis*, 20 Oct 1978, *Bowers 1547*. Side canyon immediately below the arch in Arch Canyon, canyon bottom, with lowermost *Vauquelinia*, *Rhamnus betulifolia*, and *Juniperus*, 2 Dec 1990, *Felger 90-535*. †Montezuma's Head, floret, 21,840 ybp (identified by Charlotte Reeder).

Muhlenbergia fragilis Swallen
Delicate muhly. Figure 50.

Small, delicate summer-fall ephemerals, often 10–25 cm tall. Ligules hyaline, ragged with a relatively large tooth ("auricles" or lateral extensions) on each side. Leaf blades 2–6 cm long with white, cartilaginous margins and midrib. Panicles often 8–18 cm long, 3–10 cm wide, with numerous very slender, diffuse and spreading to partially reflexed branches, freely branching at lower nodes; panicles fragile, often breaking away at maturity. Pedicels 2.5–8 mm long, straight and very slender. Spikelets slender, 1–1.2 mm long, glabrous, and awnless.

Locally common at middle to higher elevations in the Ajo Mountains; on thin soils in open areas.

Arizona mostly in the central and southeastern part of the state above the desert. Southeastern California to western Texas and southward to Oaxaca and both states of Baja California.

OP: Ajo Mt crestline, *Rutman 8 Oct 1999* (ORPI). NE slope above trail to Bull Pasture, 975 m, 22 Oct 2006, *Rutman 20061022-2*.

Muhlenbergia microsperma (de Candolle) Kunth
Little-seed muhly; *tiendrilla*. Figure 51.

Non-seasonal ephemerals, mostly encountered during winter-spring seasons but also germinating and growing with summer-fall rains, (7) 10–40 cm tall, soft and delicate, often growing through other plants or decumbent-spreading in shaded places. Roots often weakly developed. Panicles terminal, longer than wide, filmy, open and loosely flowered. Upper (larger) glumes 0.5–1.3 mm long; lemmas, tapering to a slender awn 14–28 mm long. Lower leaf axils bearing single or clustered cleistogamous spikelets (cleistogenes), these narrowly conical, awnless and without glumes, 4–10 (12) mm long, resembling a miniature cornucopia. (See *M. appressa*).

Widespread across the flora area at all elevations and in many habitats but not on dunes. Most abundant in better watered, protected microhabitats, especially among rocks, under trees, along arroyos, canyons, north- and east-facing slopes, sand flats, and playas. It has been widespread across the flora area for at least 22,000 years.

Common across the Sonoran Desert. Southwestern USA to Guatemala, and South America.

OP: Quitobaquito, *Nichol 10 Mar 1939*. Cipriano Well, Nichol 27 Apr 1939. Bates Well, 5 Mar 1940, *Benson 9913*. Walls Well, *McDougall 26 Mar 1941*. Alamo Canyon, 10 Dec 1945, *Goodding 480-45*. Aguajita, 13 Sep 1986, *Felger 86-281*. 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-5*. †Alamo Canyon, cleistogenes and florets, 9570 & 14,500 ybp. †Montezuma's Head, florets, some with awns, 13,500 to 21,840 ybp (4 samples). †Puerto Blanco Mts, 2340 to 9720 ybp (3 samples, Van Devender et al. 1990: 339).

CP: Charlie Bell Pass, 3 Apr 1992, *Whipple 3928* (CAB). Jose Juan Represo, 2 Jun 1992, *Felger 92-569*.

TA: Tinajas Altas, 19 Mar 1998, *Felger* (observation). Coyote Water, 25 Oct 2004, *Felger 04-51*. †Butler Mts, 750 ybp (Van Devender et al. 1990: 342). †Tinajas Altas Mts, 8700 to 15,680 ybp (3 samples, Van Devender et al. 1990: 341).

Figure 50. *Muhlenbergia fragilis*. Bull Pasture, 21 Sep 2008.

Figure 51. *Muhlenbergia microsperma*. Chuckwalla Hills, Organ Pipe, 6 Oct 2013.

Muhlenbergia phleoides (Kunth) Columbus
[*Lycurus phleoides* Kunth. *L. setosus* (Nuttall) C. Reeder. *Lycurus alopecuroides* Grisebach. *Muhlenbergia alopecuroides* (Grisebach) P.M. Peterson & Columbus]
Wolftail, Texas timothy. Figure 52.

Densely tufted, coarse perennials 20–60 cm tall; growing and reproductive mostly during warmer months. Leaves mostly basal, grayish green and slender; leaf tips ending in a bristle or fragile awn-like projection. Panicles spike-like and slender, mostly 3–10 cm long. Spikelets in pairs, one usually staminate or sterile and the other bisexual, the pairs falling together with the pedicels; spikelets bristly with glume and lemma awns 0.5–4 (5) mm long. Glumes 1–2 mm long, the lower glume with (1) 2 (3) awns, the upper glume with 1 awn. Lemmas 3–4 mm long, with a short, scabrous awn.

Ajo Mountains from middle to upper elevations; documented from Bull Pasture and scattered sites along the trail to Mt. Ajo.

Across most of Arizona except the lowland deserts of the far southwestern part of the state; Utah and Colorado to Oklahoma, Texas, Mexico, and Guatemala and disjunct in South America.

Muhlenbergia phleoides (*Lycurus phleoides* Kunth, described in 1815) and *M. alopecuroides* (*Lycurus alopecuroides* Grisebach, described in 1874) are distinguished on seemingly minor vegetative features, which appear to be influenced by environmental conditions. Their geographic and ecologic ranges broadly overlap and the two taxa appear to be conspecific.

OP: Bull Pasture, Ajo Mountains. *Wirt 29 Oct 1989* (ORPI). Bull Pasture area, 3185 ft, Dry, east-facing slope with shallow soils, associated species *Aristida ternipes, Bouteloua curtipendula, Cottea gracilis, Disakisperma dubium Heteropogon contortus, Hilaria belangeri,* and *Tridens muticus*, etc., 25 Sep 2013, *Rutman 20130925-8*

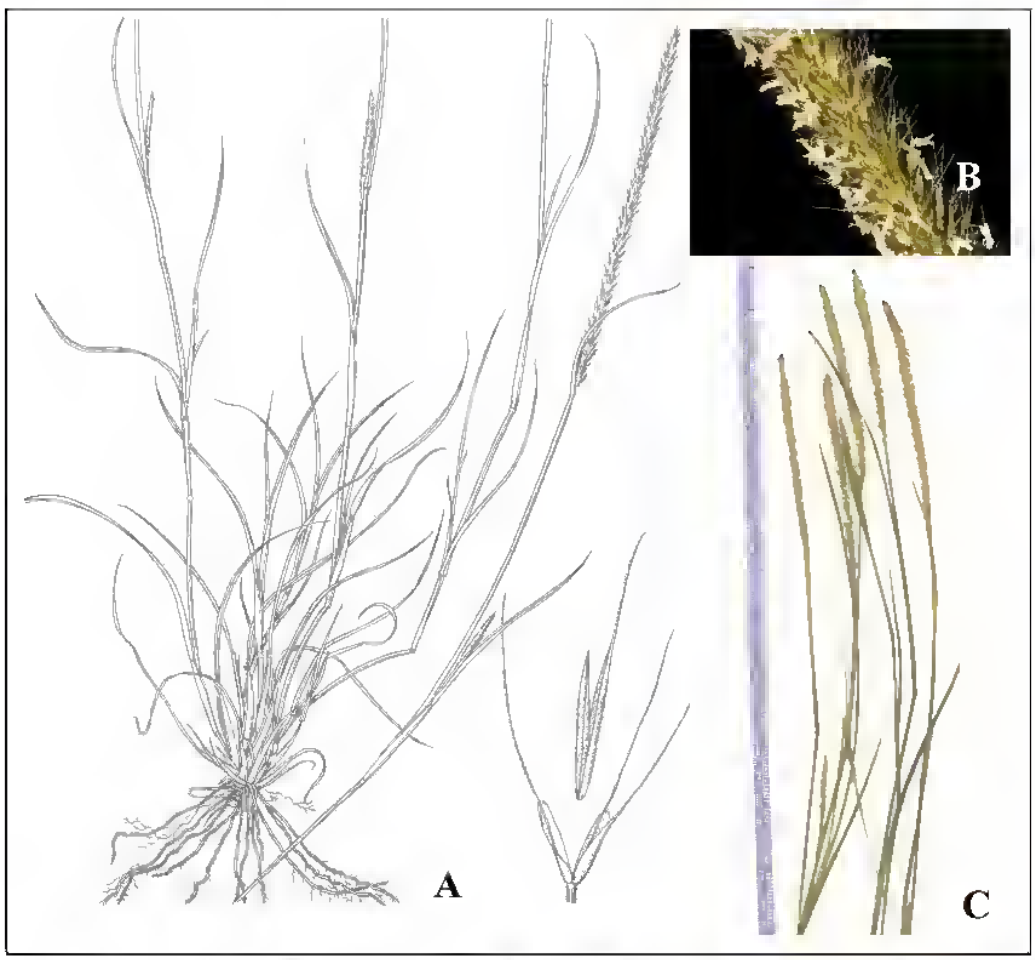

Figure 52. *Muhlenbergia phleoides*. (A) Plant and spikelet with glumes and floret separated, (B) detail of panicle, Fillmore Canyon, Organ Mts, NM, 21 Sep 2008, photo by Patrick Alexander, (C) panicles, Bull Pasture, 25 Sep 2013.

††**Muhlenbergia polycaulis** Scribner
Cliff muhly

Tufted perennials with short rhizomes. It was in the Ajo Mountains more than 29,000 years ago. The nearest known present-day population is in the Baboquivari Mountains.

Southern Arizona in non-desert areas to Texas and central and western Mexico. This species is often mistaken for *Muhlenbergia tenuifolia* (*M. monticola*) or *M. pauciflora* (Gould 1951: 211).

OP: †Alamo Canyon, florets, 29,110 ybp (identification verified by Charlotte Reeder).

Muhlenbergia porteri Scribner ex Beal
Bush muhly; *zacate aparejo*; ku:kpadag. Figure 53.

Bushy perennials often 30–80 cm tall, from a hard, knotty, semi-woody base. Culms slender, brittle, profusely branched throughout, and often interweaving. Leaf blades 1.9–6 (8) cm long and readily drought deciduous. Panicles often 6–10 cm long and about as wide, open and rather sparsely flowered; the panicles become purplish with the advent of cool weather. Mature panicles often break off as a unit and scatter in the wind like miniature tumbleweeds. Pedicels slender, 2–9 (17) mm long. Body of lemma 3.2–3.9 mm long, with an awn (2.5) 4–9 mm long. Flowering various seasons including spring and summer.

Widespread on mountain slopes to bajadas and valley floors, wash banks, and floodplains across much of Organ Pipe and the east side of Cabeza Prieta.

Widespread in the Sonoran Desert except the most arid regions. Southeastern California to Colorado and Texas, Baja California, and Sonora to the Chihuahuan Desert Region in San Luis Potosí and Zacatecas.

Bush muhly, a preferred forage of livestock, was extirpated from large areas of Organ Pipe by cattle grazing. After the cattle were removed in the late 1970s the density and cover of this grass increased substantially along the southern border of the Monument (Warren & Anderson 1987). By the mid-1980s it was common on the Arizona side of the border (eastward from 10 km east of Aguajita Spring), sometimes within a few meters of the border fence, but rare on the Sonora side of the fence due to livestock grazing. Desert tortoises often park under bush muhly plants and graze on the overhead canopy.

OP: Alamo Canyon, *Mulroy 6 Oct 1969*. 5 mi W of Visitor Center along Puerto Blanco Drive, 16 Oct 1977, *Bowers 883* (ORPI). Puerto Blanco Drive 1 mi W of Ariz Hwy 85, 23 Jul 1986, *Felger 86-227* (ORPI). W of Hwy 85 at N boundary of Monument, 23 May 1991, *Felger* (observation).

CP: Childs Mountain, 25 Feb 1993, *Felger 93-45*. Scarface Mt, steep, coarse limestone slope, 1650 ft, *Autenreith 20 Mar 1992* (ASC). *Felger* (observations). Sheep Peak, N side, mid-elevations to peak, 31 Jan 1992; 1.5 mi N of Lower Well, washes in valley plain, 25 Feb 1993.

Muhlenbergia rigens (Bentham) Hitchcock
Deer grass; *zacate del venado*. Figure 54.

Large, robust, tufted perennials to about 1 m tall. Panicles overtopping the leaves, long, slender, and spike-like, (9) 25–40 cm by usually 0.5 to less than 1 cm wide, and densely flowered. Spikelets appressed, obscuring the short, tightly appressed branches; spikelets 2.5–4 mm long, awnless or sometimes with a thick awn to 1.2 mm long. Glumes almost as long as the florets.

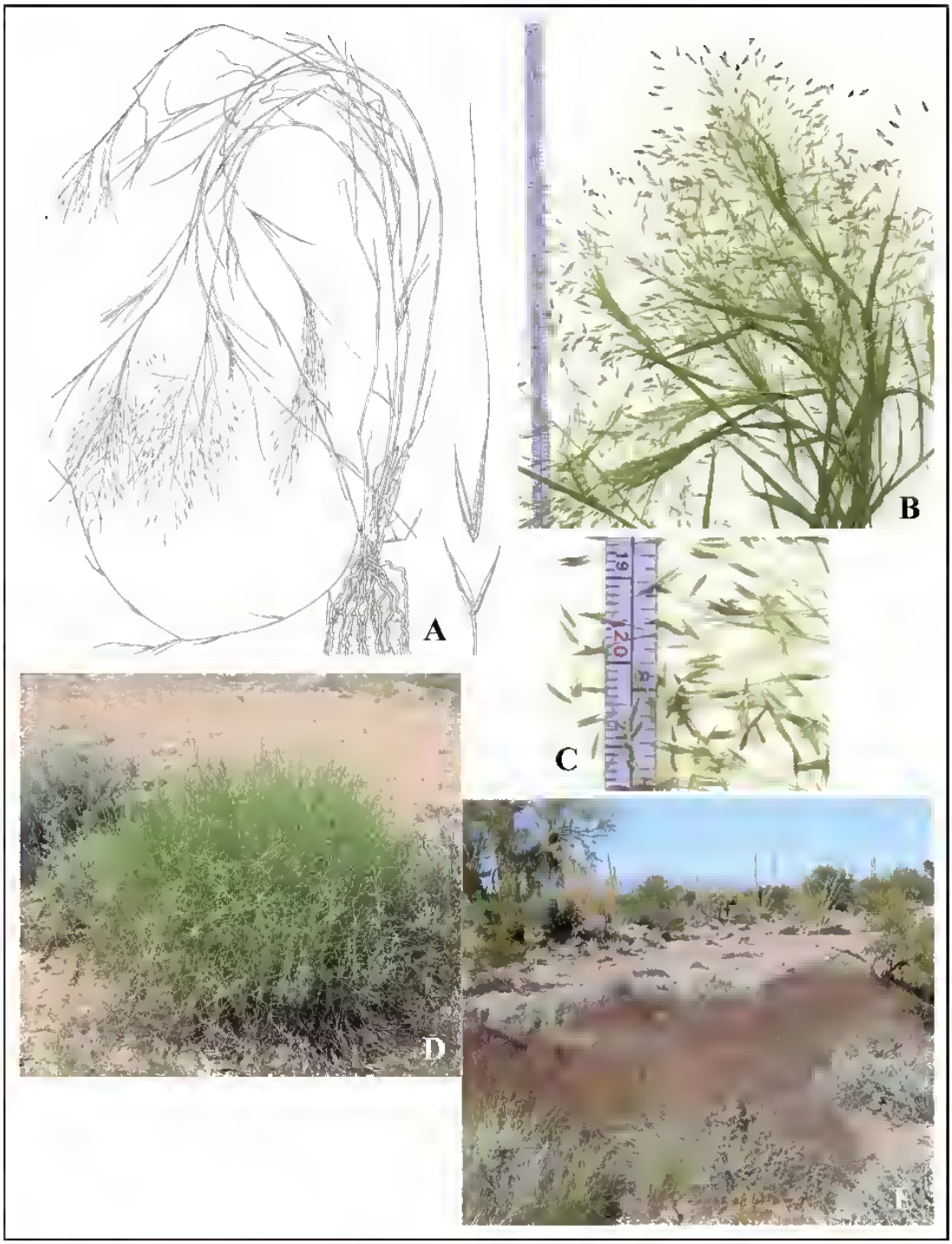

Figure 53 *Muhlenbergia porteri* (A) Plant and spikelet with glumes and floret separated, (B & C) portions of panicles, Hwy 85 at N boundary of Organ Pipe, 15 Sep 2013, (D) summer monsoon appearance, Why, Pima Co., 8 Aug 2013, (E) winter coloration, Hwy 85 near N boundary of Organ Pipe, 6 Oct 2013.

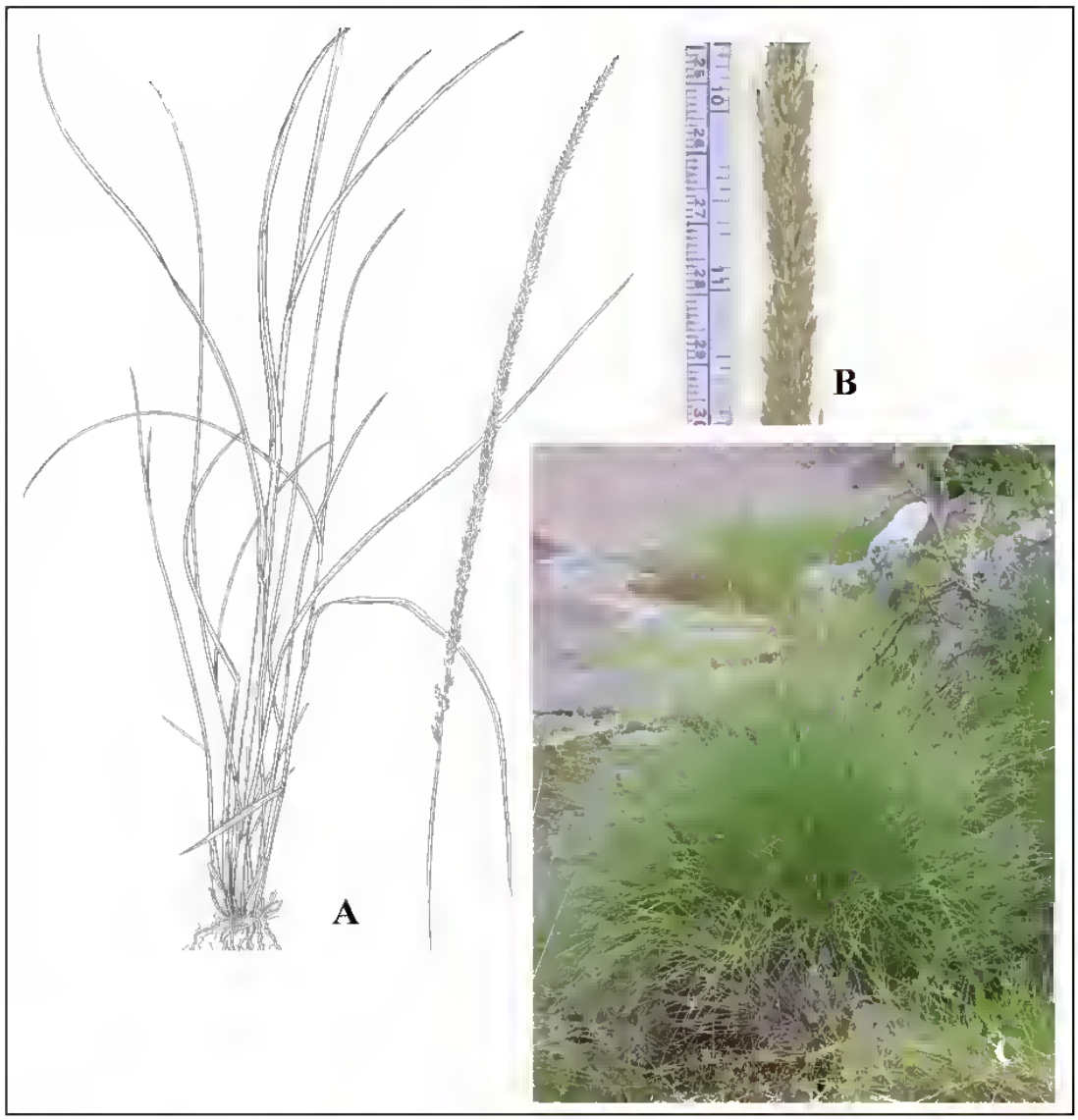

Figure 54 *Muhlenbergia rigens*. (A) Plant and panicle Alamo Canyon (B) portion of panicle, 17 Oct 2013; (C) plant, 9 Sep 2013

Ajo Mountains, recorded from Alamo Canyon along the canyon bottom where it was locally common in the scour zone near Alamo Well Tough roots anchor the plants in subsurface bedrock, allowing them to survive most scouring floods Most of the plants were removed by the scouring 500-year flood of 10 September 2012, but some survived

Widespread in Arizona, mostly above the desert Southeastern California to Texas, both Baja California states, and Sonora to Coahuila, Durango, and Jalisco

OP Alamo Canyon 2500 ft, *Nichol 14 Mar 1939*, Sandy canyon bottom, 18 Dec 1945, *Goodding 479-45*; Alamo Canyon where N & S forks meet, *Rutman 5 Mar 1995* (ORPI); Canyon bottom near ruins of ranch house, 29 Mar 2003, *Felger* (observation), Canyon bottom near Alamo Well, 21 Sep 2012, *Rutman*, observation

Muhlenbergia tenuifolia (Kunth) Kunth
[*M. monticola* Buckley]
Slender muhly, mesa muhly. Figure 55.

Figure 55. *Muhlenbergia tenuifolia*. Trail to Mt Ajo, above Bull Pasture, 16 Sep 2006.

Delicate tufted perennials, reported to be short-lived, or perhaps annuals, 25–55 cm tall. Leaf blades slender and mostly to about 10 cm long. Growing and reproductive with summer-fall rains. Panicles 8–12 (to 20?) cm long, mostly 0.5–1 (2) cm wide not including the awns, and densely flowered to somewhat open, and with short branches. Spikelets 2.5–4 mm long (excluding the awn), the lemmas conspicuously hairy towards the base with a sinuous awn to about 2.5 cm long.

Ajo Mountains, recorded from 2500 ft and common in grassy areas above 3600 ft.

Eastern and northern Arizona generally above the desert, northward to southwestern Colorado, eastward to Texas, and Mexico to northern South America.

OP: Arch Canyon, a few clumps in partial shade of overhanging cliff, 800 m, 17 Sep 1992, *Reeder 8910* (ARIZ, ASU). Saddle between Arch and Boulder canyons, 26 Oct 2003, *Rutman 20031026-23* (ORPI)

Panicum – Panic grass

Annuals/ephemerals or perennials of diverse habit. Ligules membranous-ciliate. Inflorescences panicles usually open with spikelets on long pedicels. Spikelets panicoid; awnless, with 2 florets, the lower one reduced to a sterile lemma or staminate, the upper one bisexual. Lower glume short, or at least shorter than the upper glume; upper glume and sterile lemma similar in texture. Lemma of fertile floret firm, smooth (papillose in *P. alatum*) and shiny, with inrolled margins tightly clasping the palea and enclosed grain. The spikelet may appear to have a single floret until you open it to see the characteristic sterile lemma in addition to the glumes and hard, shiny fertile lemma characteristic of panicoid grasses.

1. Summer ephemerals, usually less than 0.5 m tall, the roots often weakly developed.

    2. Upper (fertile) floret short-stipitate (stalked), the fertile lemma with two fleshy expansions (like little ears) at its base ..... **Panicum alatum**
    2. Upper (fertile) floret not stipitate, the fertile lemma without fleshy expansions ..... **Panicum hirticaule**

1. Perennials with well-developed roots.

    3. Plants usually 1–2+ m tall; panicles open with conspicuous, spreading branches drooping with weight of the grain; spikelets 2.5–3 mm long..... **Panicum antidotale**
    3. Plants less than 1 m tall; panicles contracted, the branches appressed or the inflorescence open and the branches spreading but not drooping; spikelets 2.8–4 mm long.

        4. Plants tufted, without stolons; inflorescences open, generally more than 3 cm wide, the branches spreading; glumes unequal ..... **Panicum hallii**
        4. Plants with long stolons; inflorescences slender and contracted, less than 1.3 cm wide, the branches closely appressed; glumes subequal ..... *See* **Hopia obtusa**

Panicum alatum Zuloaga & Morrone var. **alatum**
Winged panic grass

Hot-weather annuals, highly variable in size. Spikelets 2.4–3.2 mm long; upper (fertile) florets short-stalked (stipitate), strongly papillose on the entire surface and with 2 ear-like fleshy expansions at the base of the lemmas (elaiosomes); lower floret sterile.

Found in the large playas in Cabeza Prieta in clayish soils, where large populations grow during years of favorable hot-weather rains. Also in nearby Sonora and elsewhere in western Sonora in similar habitats with temporary standing water and clayish soils, especially inland playas where it is often locally abundant.

Variety *alatum* occurs in southwestern USA (southeastern California and southern Arizona) and northern Mexico to Michoacán. It has also been found along arroyos and canyon bottoms and is widespread across a wide variety of habitats in Baja California Sur. *Panicum alatum* ranges from southwestern USA to South America; Zuloaga and Morrone (1996) recognized three varieties of *P. alatum*.

Panicum alatum resembles *P. hirticaule* except for features of the spikelets: the upper (fertile) floret short-stipitate (stalked) and most noticeably the fertile lemma has a pair of elaiosomes at its base. Elaiosomes are oil-rich structures adapted for ant dispersal. The two species occupy distinct habitats and have not been found intermixed in the flora area or in western Sonora. Elsewhere they are sometimes sympatric and do not show obvious differences in geographic distribution. While the distinctions between *P. alatum* and *P. hirticaule* and their varieties are easy enough to discern with magnification, some authors treat *P. alatum* as a synonym of *P. hirticaule* subsp. *hirticaule* (e.g., Freckmann & Lelong 2003).

CP. Pinta Playa, *Edwards 9 Oct 1977*. Las Playas, 28 Nov 2001, *Felger 01-555*.

***Panicum antidotale** Retzius
Giant panic grass, blue panic grass; *panizo azul*. Figure 56.

Robust perennials mostly 1–2+ m tall, with hard knotty bases, short rhizomes, tough roots, and woody-based culms. Branching and leafy from near the base to the upper part of the plant. Leaves often bluish glaucous. The above-ground part of the plant may die back to the rhizomes during the winter. Panicles mostly terminal, open with conspicuous, spreading branches drooping with weight of the grain; spikelets 2.5–3 mm long, the lower floret staminate. Reproductive during warm weather.

Common in drainages along the international border east of Lukeville, spreading from adjacent agricultural areas in Sonora. It was rather rare in Organ Pipe in 1987, but by the late 1990s it had become common northward at least 1 km from the border in gully bottoms and swales of sandy loams. Giant panic grass also was established in roadside ditches at Why at least from the 1980s to 1992, but it was no longer present in 2012.

Native to India, grown as a forage grass and adventive in southwestern USA and tropics worldwide.

OP. 2 mi E of Lukeville, 15–20 m N of border fence, about one dozen plants with *Cynodon*, *Setaria macrostachya*, and *Salsola*, 11 Nov 1987, *Felger 87-329*. E of Lukeville, 1.6 mi E of Border Monument 166, *Rutman 29 Aug 2001* (ORPI). Near the U.S./Mexico boundary, NW of Gachado line camp, fine sandy loam, in a shallow depression where water settles, with *Cenchrus ciliaris*, *Rutman 8 Aug 2005*

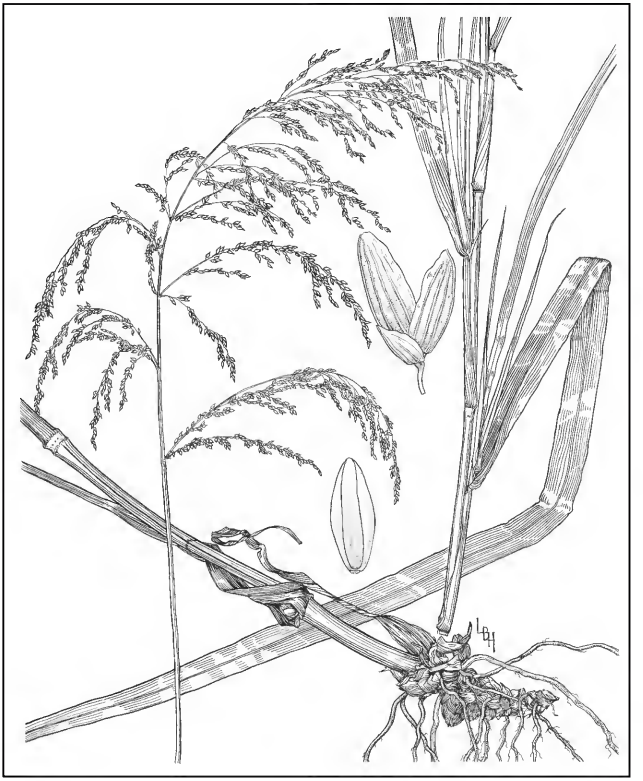

Figure 56. *Panicum antidotale*. Plant, panicle, fertile floret (below), and spikelet (above) spread open showing the smaller lower glume, upper glume (right), and sterile lemma.

Panicum bulbosum, see **Zuloagaea bulbosa**

Panicum hallii Vasey var. **hallii**
[*P. lepidulum* Hitchcock & Chase]
Hall's witchgrass

Tufted perennials, sparsely hairy, the basal leaves often curly like slender wood shavings. Plants glaucous bluish-green. Spikelets often 3–4.2 mm long; lower glumes ½–¾ as long as the spikelets; lower floret sterile. Growing and reproductive during warm weather.

Documented in the flora area by a single specimen from the Ajo Mountains in 1938. This or a similar panic grass grew in the Puerto Blanco Mountains about 1000 years ago and in the Ajo Mountains 20,500 years ago. The nearest records are from Sierra El Humo, WSW of Sasabe, Sonora (*Van Devender 2005-841*) and Table Top Mountain in Pinal County (*Felger 02-58*).

Eastern and southern Arizona, mostly at elevations above the desert. Southwestern USA to central Mexico. Another variety occurs in Texas and northeastern Mexico and has been found in California, almost certainly as a weed (Riverside Co, 20 mi W of Blythe, 11 Sep 2012, *Rink 11695*, ASC).

OP: Ajo Mts, *Goodding 31 Oct 1938*. †*P.* cf. *hallii*: †Puerto Blanco Mts, 980 ybp (Van Devender et al. 1990: 339). †Montezuma's Head, florets, 20,490 ybp.

Panicum hirticaule J. Presl subsp. **hirticaule**
[*P. capillare* Linnaeus var. *hirticaule* (J. Presl) Gould]
Mexican panicgrass. Figure 57

Figure 57. *Panicum hirticaule*. (A & B) Young flowering plants, Alamo Canyon, 15 Sep 2013, (C) spikelet spread apart showing glumes and sterile lemma (below) and fertile floret (above), (D) portion of plant showing pubescence, Alamo Canyon 12 Sep 2008

Summer ephemerals, highly variable in size, (5) 20–60 cm tall (sometimes much taller elsewhere), often with a single main axis; roots often weakly developed. Plants usually with prominent, spreading, coarse and usually bulbous-based hairs, especially on stems, leaf sheaths, lower leaf-blade surfaces, or rarely glabrate or glabrous; flowering branches and spikelets glabrous. Panicles erect, the branches mostly straight, or drooping with weight of the grain on large, robust plants with especially large panicles. Spikelets 2–4 mm long. Lower glumes 1.5–2 mm long, ½–¾ as long as the spikelets; glumes and lemmas with conspicuous longitudinal (parallel) green veins. Lower floret sterile. Fertile lemmas smooth and shiny, 1.6–2 × 0.7–1 mm, shiny cream-white, becoming dark brown with age.

Often common along major drainageways and also on rocky slopes, sandy plains, and many other habitats. Widespread and seasonally common nearly throughout Organ Pipe and at least the eastern part of Cabeza Prieta. Documented in the Ajo Mountains for 20,500 years, these fossils clearly are subsp. *hirticaule*.

Widespread in the Sonoran Desert; southwestern USA to South America and the West Indies.

OP: Washes N of Customs House, 27 Aug 1943, *Clark 10904* (ORPI). Alamo Canyon, 18 Dec 1945, *Goodding 475-45*. Estes Canyon, 20 Aug 1950, *Supernaugh 448*. Aguajita Wash, 14 Sep 1988, *Felger 88-428*. Growler Wash, *Wirt 2 Aug 1990* (ORPI). E of Armenta Ranch, *Rutman 30 Sep 2006*. †Alamo Canyon, florets, 1150 to 9570 ybp (3 samples). †Montezuma's Head, florets, 13,500 & 20,490 ybp.

CP: Daniels Arroyo at Charlie Bell Rd, 18 Aug 1992, *Felger 92-657*. San Cristobal Wash, 14 Sep 1992, *Felger 92-690*.

Panicum obtusum, see **Hopia obtusa**.

Pappophorum vaginatum Buckley
[*P. apertum* Munro ex Scribner. *P. subbulbosum* Arechavaleta. Not *P. vaginatum* Philippi]
Pappus-grass; *puntiagudo barbón*. Figure 58.

Robust, tufted perennials, often about 50–70 cm tall, essentially glabrous. Inflorescences of panicles overtopping the leaves, often whitish, slender and densely flowered, often 15–18 × (0.8) 1–1.5 cm. Spikelets with 3 florets, the lower ones bisexual, the upper ones reduced. Glumes translucent, 1-veined, awnless or rarely with an awn to 1 mm long. Fertile lemmas plump, with multiple veins and lobes extending into 10 or more stiff, scabrous (not plumose) unequal awns often 5–6.5 (7) mm long, the awns mostly spreading at right angles at maturity and longer than the lemma body.

Locally in Bull Pasture and probably elsewhere in the Ajo Mountains.

The nearest records are from the vicinity of Why and eastward and the Vekol Valley in the Sonoran Desert National Monument, usually in low-lying, fine textured soils of valley bottoms. Eastward in southern Arizona to Texas and northern Mexico, disjunct in Argentina.

OP: Ajo Mts, *Albee Apr 1937*. Bull Pasture, 3100 ft, small patch with *Panicum obtusum*, 24 Sep 2006, *Rutman 20060924-2*.

Figure 58. *Pappophorum vaginatum* (A) Plant and panicle, (B & C) Bull Pasture, 25 Sep 2013; (D) Hwy 86 roadside east of Why, Pima Co , 21 Sep 2012.

Pappostipa speciosa (Trinius & Ruprecht) Romaschenko
[*Achnatherum speciosum* (Trinius & Ruprecht) Barkworth *Jarava speciosa* (Trinius & Ruprecht) Peñailillo *Stipa speciosa* Trinius & Ruprecht]
Desert needle-grass Figure 60

Tufted perennials often 65–75 cm tall with a dense basal clump of leaves. Leaf sheaths reddish brown, ligules densely ciliate with a tuft of hairs on each side of the collar (ligules in this species reported to be variable among different leaves, some perhaps less hairy or glabrous, e.g., Arriaga 2007), leaf blades tough and inrolled, the longer one often 45–60 cm, and less than 1 mm wide when dry. Dormant during the cooler months as well as the hotter months, growing and reproductive March–May and in fall. Inflorescences of panicles 10–26 cm long, contracted, densely flowered and spike-like, young, emerging panicles and lower part of mature panicles partially enclosed by a broad leaf sheath. Spikelets readily separating above the glumes, and with 1 floret. Glumes 13–20 mm long, longer than the lemma body, elongated and tapering, papery, and persistent. Lemmas firm at maturity with overlapping margins, tightly enclosing the palea, and bearing a stout, persistent terminal awn 3.3–4.5 cm long, with 1 bend (once geniculate), the awn column strongly twisted and bearded (plumose) below the bend with slender white hairs (3) 5–6 (8) mm long, awn and body of lemma of different textures and colors, the junction abrupt.

Figure 60 *Pappostipa speciosa*. Alamo Canyon (A) 16 Sep 2006, (C) 17 Oct 2013 (B) Near village of Kuakatch, Organ Pipe, 24 Mar 2013

Canyons and mostly north-facing slopes in the Tinajas Altas Mountains and common at middle to upper elevations in the Ajo Mountains, especially along the crestline, often growing out of rock crevices on north- and east-facing slopes.

Southern California to Colorado and Arizona, both Baja California states, and northwestern Sonora, and disjunct in Chile and Argentina. The type locality is in Chile. "Several varieties are recognized in South America. It is not clear to which of these varieties, if any, the North American plants belong" (Arriaga 2007: 181).

Desert needle-grass has grown in mountains across the flora area for at least 11,000 years. Its maximum distribution seems to have been in the early Holocene. This grass, like the Joshua tree, is now widespread in the Mohave Desert and seems to have expanded northward into Nevada in the early Holocene.

OP: Sierra de Alamos, *Nichol 16 May 1937*. Alamo Canyon, *Nichol 4 May 1939*. Arch Canyon, 3 May 1978, *Bowers 1301*. Bull Pasture, 3215 ft, 9 Apr 2005, *Felger 05-183*. Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger* (observation). †Alamo Canyon, florets, 8130 to 9570 ybp (3 samples). †Puerto Blanco Mts, 7970 ybp (Van Devender et al. 1990: 339).

TA: Tinajas Altas, *Van Devender 26 Mar 1983*. Borrego Canyon, 16 Jun 1992, *Felger 92-616*. †Butler Mts, 3820 & 10,615 ybp (Van Devender et al. 1990: 341–342). †Tinajas Altas Mts, 5860 to 10,950 ybp (7 samples, Van Devender et al. 1990: 341)

††**Paspalum** sp.

A single, well-preserved floret 2.2 mm long, from an Ajo Mountain midden 22,000 years old, was identified by John Reeder. It is perhaps *P. setaceum* Michaux var. *stramineum* (Nash) D.J. Banks. No member of this genus is known to occur in the flora region today. This large and widespread genus generally occurs in wetland places in the Sonoran Desert Region. The nearest modern populations are along the lower Gila and Colorado Rivers.

OP: †Montezuma's Head, 21,840 ybp.

***Phalaris** – Canary Grass

Winter-spring ephemerals in the Sonoran Desert Region. Panicles ovoid to cylindrical and densely flowered. Spikelets breaking off above the glumes, laterally compressed, and awnless, with 1 bisexual (fertile) floret and 1 or 2 (those in the flora area) small, scale-like sterile florets below, these falling with the fertile floret. Fertile lemma tightly enclosing the palea and grain.

1. Keel of glumes scarcely winged and neither notched nor toothed; sterile florets 2 ..... **Phalaris caroliniana**
1. Keel of glumes conspicuously winged and often notched or toothed; sterile florets 1 ..... **Phalaris minor**

***Phalaris caroliniana** Walter
Carolina canary grass; *alpistillo*. Figure 61A.

Known in the flora area from a single record at Las Playas and perhaps locally established. The nearest known record is from a heavily grazed playa in the Pinacate Region (Rancho los Vidrios) in nearby Sonora (Felger 2000).

Native in eastern USA and naturalized in many parts of the world.

CP: Las Playas, under mesquite, in channels, not common, 1 Mar 1998, *Harlan 494*.

***Phalaris minor** Retzius
Little-seed canary grass; *alpistillo silvestre*, ba bkam Figure 61.

Plants highly variable in size. Panicles spike-like, mostly several centimeters long, sometimes 8–10 cm long. Glumes 4.5–5.5 mm long, the keel expanded into a wing often notched or with small irregular teeth. Fertile lemmas 3–3.5 mm long, broadly ovate-lanceolate, and hairy.

Figure 61. *Phalaris*. (A) *P. minor*, plant, panicle, glumes and fertile floret with reduced single sterile floret (below) and *P. carolinana* spikelet (above), (B) *P. minor*, below Gillespie Dam, Maricopa Co., 31 Mar 2013, (C) *P. minor*, Hwy 85 near Organ Pipe visitor center, 7 Apr 2008.

Often in locally dense stands at waterholes and dirt tanks, and major washes on the east side of Cabeza Prieta, where large stands of this grass often grow in drying mud above stagnant water of dirt tanks (*charcos*). It is apparently not eaten by deer, javelina, or jackrabbits. In years of favorable rains it is abundant in Organ Pipe, mostly in xeroriparian areas.

Native to the Mediterranean region; widely naturalized in the Sonoran Desert region and elsewhere in the world.

OP: Growler Canyon, 30 Mar 1979, *Bowers 1603*. 2-way section Puerto Blanco Drive, 2 mi W of Hwy 85, roadside, 10 May 1979, *Bowers 1722*. Gachado Line Camp, 11 Nov 1987, *Felger 87-328*. Cuerda de Leña at N boundary, *Rutman 16 Mar 1995* (ORPI). Ruin of ranch building near mouth of Alamo Canyon, 29 Mar 2003, *Felger 03-397*. Cherioni Wash 100 ft W of Rte 85, *Casper 10 Apr 2003* (ORPI). Hwy 85, roadside, imported by ADOT in straw used as mulch, N of park headquarters, 9 Apr 2005, *Felger 05-160*.

CP: San Cristobal Wash, 20 Mar 1992, *Harlan 55* (CAB). Agua Dulce Mts, localized colony in sandy-gravel soil in canyon bottom near the tank, 13 Jun 1992, *Felger 92-579A*. *Felger*, observations: Redtail Tank, 12 Jun 1992; Antelope Tank, 13 Jun 1992; Charlie Bell Rd at Daniels Arroyo, 10 Apr 1993.

Phragmites australis (Cavanilles) Trinius ex Steudel subsp. **berlandieri** (E. Fournier) Saltonstall & Hauber
[*P. communis* Trinius]
Common reed, reedgrass; *carrizo*; va:pk. Figure 62.

Figure 62. *Phragmites australis*. Growing among *Tessaria sericea*, Williams Spring, 31 Jan 2013.

Bamboo-like perennials reeds reaching about 3 m in height, with strong rhizomes and tough roots. Major culms stout, reaching 10–15 mm diameter, and also often producing numerous smaller branched culms as slender as 1.7 mm diameter. Leaf blades (7) 30–40 cm long. Reproductive at least July to October. Inflorescences of terminal, plume-like, and densely flowered panicles Spikelets with several florets, the glumes unequal, the upper florets reduced; spikelets usually break off below the long-bearded rachillas, which aid in wind dispersal. Rachillas with long silky white hairs, the lemmas glabrous; glumes unequal. Birds flying between wetlands and waterholes are likely dispersal agents.

Small but well-established colonies occur in wet soil at the Burro and nearby Williams Springs, northwest of Quitobaquito, growing with *Tessaria sericea* and *Prosopis glandulosa*. Several large, local populations occur nearby along the Río Sonoyta in Sonora (Felger 2000).

Phragmites australis occurs on every vegetated continent on earth and is one of the world's most widespread species of flowering plants. Three subspecies are recognized; subsp. *berlandieri*, known as the Gulf Coast lineage, ranges across southernmost USA and through Mexico to South America.

OP: Burro Spring 4 May 1978, *Bowers 1316* (ORPI), 23 Jul 1986, *Felger 86-214*, 24 Oct 1987, *Warren 87-110* Williams Spring, hypersaline, wet through most of the year, with *Pluchea sericea*, *Tibbitts 13 Feb 2013*

Poa – Bluegrass; *zacate azul*

The two species found within the Sonoran Desert are cool-season ephemerals (elsewhere this large genus of about 500 species includes annuals and mostly perennials). Ligules membranous; leaf blades with a boat-shaped tip (sometimes described as "prow-shaped" or "navicular"). Inflorescences of terminal panicles. Spikelets 2–8 florets, awnless, laterally compressed, breaking apart above the glumes and between the florets. Uppermost florets reduced or rudimentary. Lemmas 5-veined, often with a cottony, cobwebby tuft of hair.

Poa and *Festuca*, each with about 500 species, are the largest genera of grasses and worldwide in distribution. Except for the four ephemeral species listed in this flora, these genera are essentially absent from the Sonoran Desert and there are relatively few species in deserts elsewhere.

1. Spikelets mostly 3.6–4.6 mm long; lemmas 2.1–2.7 mm long, glabrous to slightly hairy on veins but without a cottony web; well-watered disturbed habitats, probably extirpated from the flora area ..... **Poa annua**
1. Spikelets mostly 4.5–6.5 mm long; lemmas 3.2–4 mm long with a cottony web at base; desert habitats and roadsides ..... **Poa bigelovii**

****Poa annua** Linnaeus

Annual bluegrass, winter-grass; *pastito de invierno*

Winter-spring annuals; plants small, soft, glabrous, and bright green.

Collected at Quitobaquito in 1945 when the site was inhabited and not recorded there since. It grew in the marsh around the pond with *Myosurus* and *Veronica*. The local demise of this water-loving weedy little grass is probably due to the increase in vegetation cover since the domestic livestock were removed. It occurs as a winter lawn and garden weed in nearby Sonoyta.

Native to the Old World and weedy and naturalized worldwide.

OP: Quitobaquito, marsh around reservoir, 17 Mar 1945, *Darrow 2405*

Poa bigelovii Vasey & Scribner
Bigelow bluegrass; *zacate azul precoz.* Figure 63.

Winter spring ephemerals, (8) 12–55 cm tall, with delicate slender and erect culms and panicles, the roots often weakly developed. Spikelets pale green, 4.5–8 mm long, with 3–8 florets, the young spikelets spear-shaped, the spikelet base with a dense cottony tuft or web. Florets at first overlapping and compressed (flattened) against each other, spreading apart at maturity with the floret margins becoming visible. Lemmas 3.2–4.4 mm long, the margins membranous and with white hairs.

Figure 63. *Poa bigelovii*. (A) Kuakatch Wash near Organ Pipe east boundary, 24 Mar 2013; (B) Alamo Well, 6 Feb 2005.

Washes, floodplains, and rocky slopes to higher elevations; fairly common and widespread during years of favorable winter-spring rains across Organ Pipe but scarce in the more arid southwestern corner, and also seasonally common in the eastern part of Cabeza Prieta. It has been in Organ Pipe for at least 20,500 years.

Widespread in Arizona. This is the only native *Poa* in the Sonoran Desert. Southwestern USA, Baja California and Sur, and Sonora to Chihuahua, Coahuila, and Nuevo León.

OP: Dripping Springs, 17 Mar 1945, *Darrow 2444*. Alamo Canyon, 12 Apr 1978, *Bowers 1250*. 0.6 mi E of Lukeville, 20 Feb 1988, *Felger 88-04*. Aguajita, 3 Mar 1992, *Felger 92-111*. Trail from The Cones to Mount Ajo, 4100 ft, 10 Apr 2005, *Felger* (observation). †Montezuma's Head, 20,490 ybp.
CP: Agua Dulce Pass (plants dry and dead), 13 Jun 1992, *Felger 92-574*. Charlie Bell Rd just W of E boundary of Refuge, 25 Feb 1993. Childs Mt, 9 Apr 1993, *Felger 93-291*.

††**Poa fendleriana** (Steudel) Vasey
Mutton bluegrass

Tufted perennials. Male and female flowers usually on separate plants.

Mutton bluegrass grew in the Ajo Mountains during the last Ice Age (Soreng & Van Devender 1989). Today this species in Arizona occurs in woodland and forested areas, mostly above 5000 ft but occasionally descending to 3500 ft. The nearest present-day population is in the Baboquivari Mountains. Gould (1951: 70) reported that it "produces relatively small amounts of viable seed." Western North American from Canada to Mexico.

OP: Alamo Canyon, 14,500 ybp. Montezuma's Head, 20,490 & 21,840 ybp.

***Polypogon**
Ephemeral/annuals and potentially perennials. Leaf blades flat, thin, and bright green. Inflorescences of panicles densely flowered and contracted or with short branches and densely to loosely flowered. Spikelets small, with 1 floret, breaking away below the glumes; spikelets with a pedicel-like stipe. Glumes longer than the florets. Lemmas membranous, 5-veined.

1. Ephemerals; spikelets awned ..... **Polypogon monspeliensis**
1. Ephemeral/annuals (and potentially perennials); spikelets awnless ..... **Polypogon viridis**

***Polypogon monspeliensis** (Linnaeus) Desfontaines
Rabbitfoot grass; *zacate cola de zorra*. Figure 64.

Non-seasonal ephemerals. Highly variable in size depending upon soil moisture. Leaf blades 3.5–22 × 0.5–1 cm. Panicles densely flowered, appearing furry like a rabbit's foot, (1.5) 3–15 cm long, with white to tawny-brown awns. Glumes 1.5–2.2 mm long, each with a slender awn 4–7 mm long. Lemmas and paleas thin, translucent, slightly exceeding the grain, the lemmas with a delicate, deciduous awn 1 mm long. Reproductive at least April to October.

Common in moist to wet, often alkaline soil near springs and seeps in the Quitobaquito region and near water in Alamo Canyon, and one record from Cabeza Prieta. Normally a wetland plant, *P. monspeliensis* grew along Highway 85 in 2005, the seed being present in the "certified weed-free" straw originating from California and used as mulch in construction zones by the Arizona Department of Transportation; these plants did not persist.

Native to Europe, widely naturalized in the Sonoran Desert and elsewhere in western North America, mostly in wetland habitats.

Figure 64. *Polypogon monspeliensis*. (A) Below Gillespie Dam, Gila River, 31 Mar 2013; (B) Ajo Mountains Wayside, Hwy 85, 29 Apr 2009; (C) seasonally wet swale, Quitobaquito, 5 Apr 2008.

OP: Quitobaquito, *Nichol 28 Apr 1939* (ORPI). Rincon Spring, 13 Apr 1941, *McDougall 91*. Alamo Canyon, *Tinkham Apr 1942*. Burro Spring (with *P. viridis*), 23 Jul 1986, *Felger 86-215b*. State Route 85, N of park headquarters, area of roadside construction as seed mixed with the "weed-free" straw used as mulch, 9 Apr 2005, *Felger 05-162* (ASU).

CP: Near Agua Dulce seep, Agua Dulce Mts, *Henry* 05/08/1996 (CAB).

***Polypogon viridis** (Gouan) Breistroffer
[*Agrostis semiverticillata* (Forsskål) C. Christensen. *Polypogon semiverticillata* (Forsskål) Hylander]
Water bentgrass. Figure 65.

Ephemeral/annuals and sometimes perennials with creeping rhizomes or stolons, the culms often reaching 30–40 cm long, decumbent to erect, rooting at the lower nodes. Leaf blades flat, 5.5–14 cm × 3.5–13 mm. Panicles 5–8 (12) cm long, compact or sometimes interrupted and with a few

branches, or sometimes rather loosely and much branched. Spikelets awnless. Glumes 1.4–2.1 mm long, minutely scabrous and appearing speckled, membranous and translucent with a broad green midstripe or sometimes partially or all purplish. Lemmas 0.8–1 mm long. Growing and flowering March through the warmer months.

Localized, dense colonies in wet mud at periphery of the *Phragmites* colony at Burro Spring and at Quitobaquito in wet mud and shallow running water at springs and ditches leading into the pond. In the 1980s and 1990s it was well established at Quitobaquito, where it seemed to be competing successfully with the similar-looking *Cynodon dactylon* and *Distichlis spicata* in ditches with running water. The nearest known population is at Quitovac in northwestern Sonora.

Native to the Old World and widely naturalized in western North America.

OP: Burro Spring: Moist soil, with *Pluchea sericea* & *Prosopis glandulosa*, 4 May 1978, *Bowers 1311*, Common perennial, wed mud at periphery of Phragmites colony, 13 Jul 1986, *Felger 86-215*. Quitobaquito: Moist soil of marsh, 17 Mar 1945, *Darrow 2409*; Emergent from shallow water and very wet soil along water ditch, *Scirpus americanus*, *Distichlis spicata*, 6 Apr 1988, *Felger 88-318*; Common along shaded channel N of pond, with *Polypogon monspeliensis*, *Cynodon dactylon*, and *Eleocharis rostellata*, shaded by *Prosopis velutina* and *Ziziphus obtusifolia*, 5 Apr 2013, *Rutman 20130405-2*.

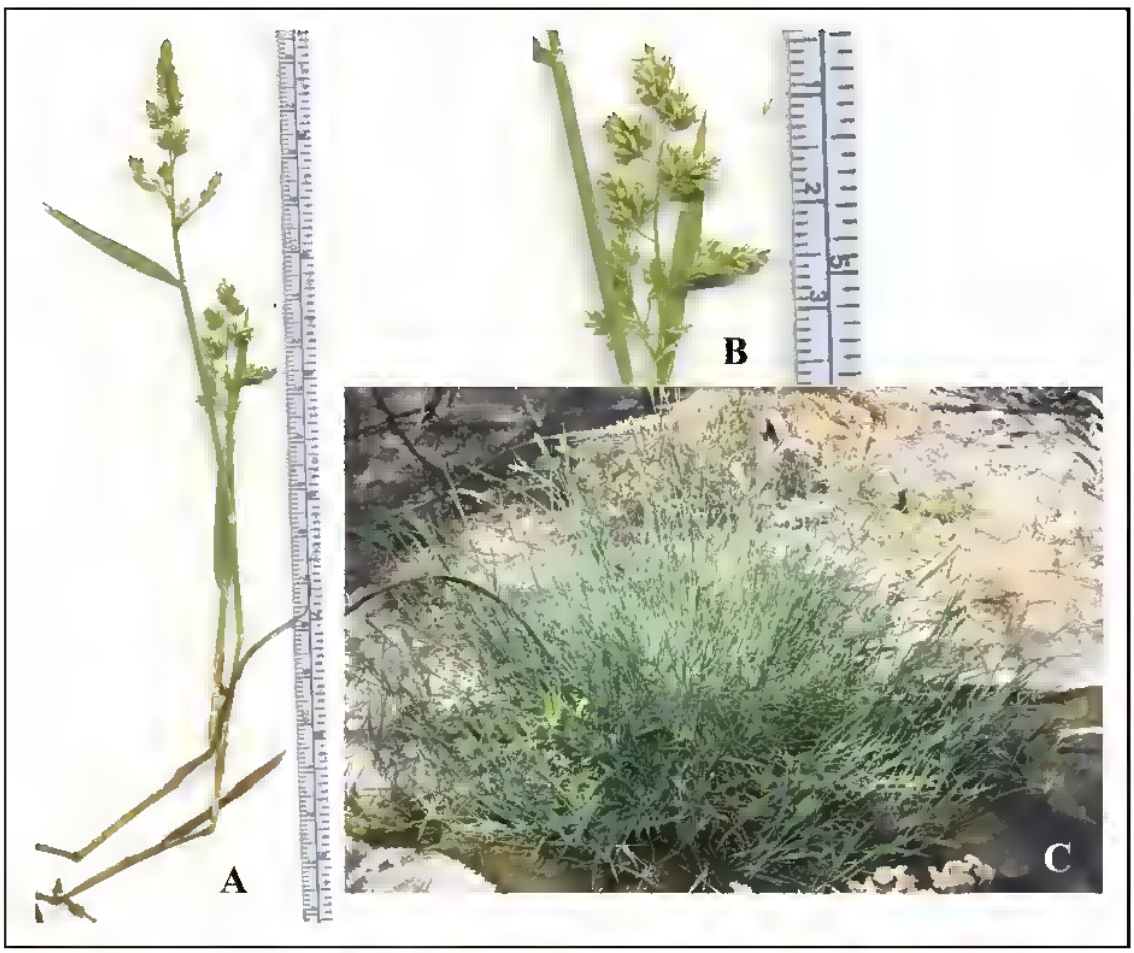

Figure 65. *Polypogon viridis*. Quitobaquito. (A & B) 11 Sep 2008, (C) 5 Apr 2013.

Schismus – Mediterranean and Arabian grasses

Small winter-spring ephemerals. Culms erect to often spreading or semi-prostrate. Leaves mostly basal, the blades bright green and narrow. Inflorescences of compact panicles. Spikelets with several florets, awnless, breaking apart above glumes and between florets. Glumes longer than the lemmas, with membranous white margins. Native to the Old World

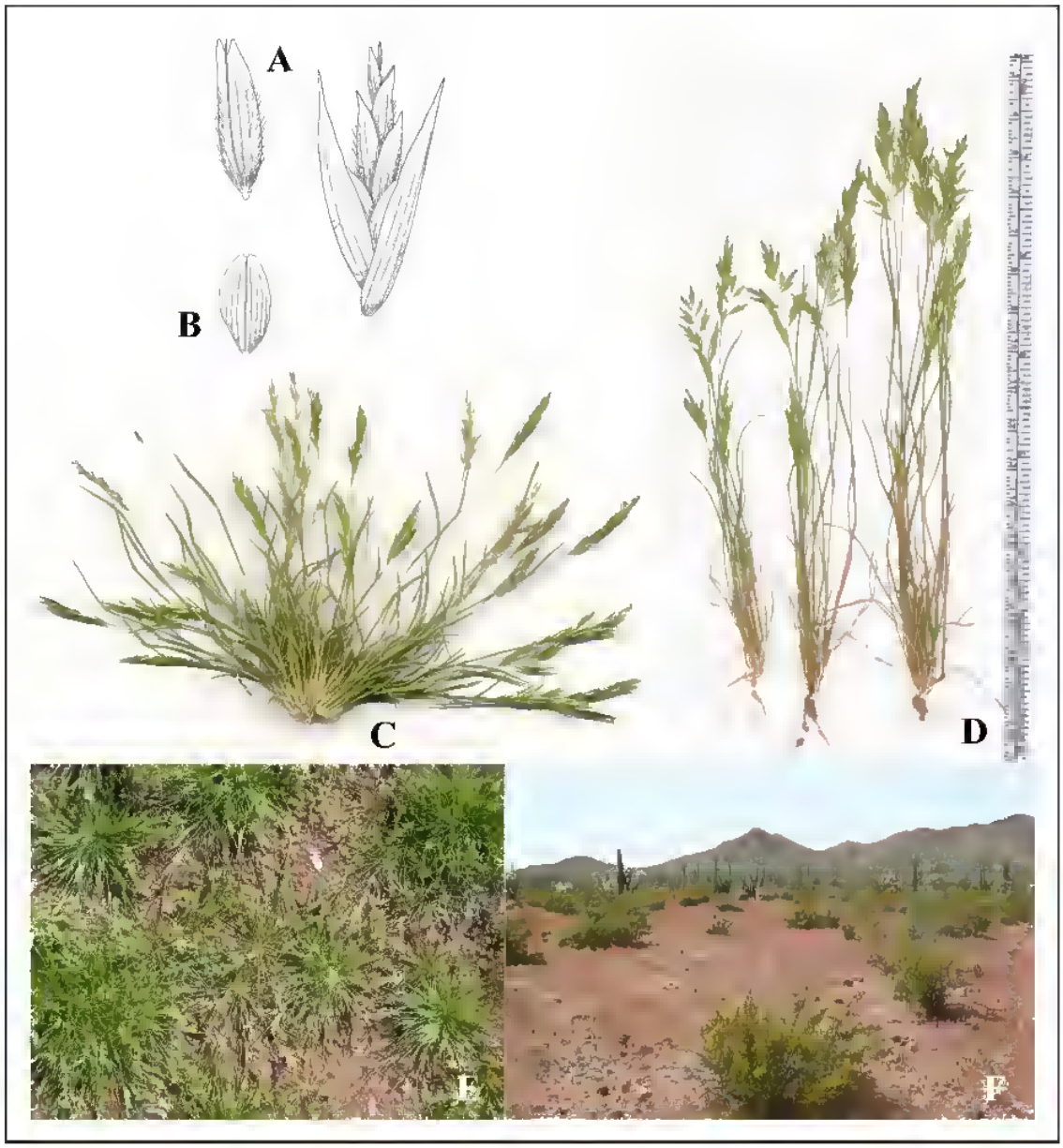

Figure 66. *Schismus*. (A) *S. arabicus*, spikelet and lemma, and (B) *S. barbatus*, lemma, (C) *S. barbatus*, Armenta Ranch area, 4 Apr 2002, (D) *S. barbatus*, upright form, Estes Canyon, 3 Apr 2010, (E) prostrate form, Armenta Ranch area, 13 Feb 2005, (F) plants turn reddish as they senesce, (creosotebush in foreground), NW of Bates Mts, 20 Mar 2005.

The two species, distinguished by subtle differences in the spikelets, are widely established in arid and semi-arid regions of the world. These little grasses are ubiquitous across the Sonoran Desert and can become abundant, sometimes to the near exclusion of native ephemerals (Felger 1990, 2000; Felger et al. 2003). *Schismus* germinates and grows rapidly with cool-weather rains. The culms and leaves often spread close to the ground, especially in open, arid sites and during cooler weather early in the season, effectively excluding or preventing other ephemerals from sprouting (Felger 2000). The spreading-prostrate habit may also function much like the rosette, first leaves of many dicotyledonous winter-spring ephemerals. Upright growth forms are also common, especially in shaded places and later in the season in warmer spring weather.

Both species of *Schismus* are seasonally common across much of the flora area, although they seem to replace each other with respect to the Lower Colorado Valley–Arizona Upland boundaries (Felger 2000). Similar eco-geographic segregation also occurs in their native habitat as well as the Middle East (Conert & Türpe 1974; Feinbrun-Dothan 1986).

Seasonally dense growth of *Schismus* grasses can fuel fires. The Tule Fire of 2005 in Cabeza Prieta National Wildlife Refuge was carried by heavy winds and ample fuel loads of *S. arabicus* and the native woolly plantain (*Plantago ovata*) (Felger et al. 2007b; Curtis McCasland, pers. comm. to R. Felger 2005). During years of favorable rain, high-density stands of taller than usual *Schismus* can interfere with the movement of lizards. Sue Rutman observed lizards near Gachado Ranch during the 1997 winter season "swimming" over the top of dense *Schismus* about 15 cm tall rather than attempting ground navigation.

1. Lemmas hairy on back and margin; palea shorter than the lemma, usually not reaching the lemma notch ..... **Schismus arabicus**
1. Lemmas glabrous over back (occasionally with few hairs near the base) or with some hairs on margins; palea about as long as the lemma ..... **Schismus barbatus**

***Schismus arabicus** Nees
[*S. barbatus* subsp. *arabicus* (Nees) Marie & Weiller]
Arabian grass. Figure 66.

Culms and panicles (4) 10–20 (22) cm long. Lemmas 1.5–2.4 mm long, pubescent, the tip notched, the lobes often pointed (acute).

Most abundant on sandy soils of sand flats, arroyos and washes, interdune troughs, and bases of larger dunes, but also common on rocky soils and hills. Lower Colorado Valley region, from the western part of Organ Pipe westward through Cabeza Prieta and Tinajas Altas.

Native from southwestern Africa to the western and northern Sahara and the western Mediterranean Region.

OP: N of Pozo Nuevo, 30 Mar 1978, *Bowers 1109*. Growler Canyon, 1.5 mi E of Bates Well, *Wirt 24 Apr 1989*.

CP: W of Namer's grave site, 14 Mar 1983, *Reeder 7590*. Growler Mts above Charlie Bell Wash, 3 Apr 1992, *Whipple 3927*. Charlie Bell Rd at Daniels Arroyo, 9 Apr 1993, *Felger 93-358*. E Pinta Sands, 11 Apr 1993, *Felger 93-411*. Childs Mt, 5 Mar 1994, *Felger 94-15*.

TA: Tinajas Altas, *Van Devender 5 Mar 1983*. Coyote Water, 21 Feb 2005, *Felger 05-154*.

***Schismus barbatus** (Linnaeus) Thellung
Mediterranean grass. Figure 66.

Resembling *Schismus arabicus* but the glumes tending to be slightly shorter, the lemma usually glabrous on the back or with hairs on the margins or occasionally near the base, the apical notch of the lemma often shallow or minute and the lobes variously obtuse or not, and the palea about as long as the lemma.

Widespread across Organ Pipe in the Arizona Upland including mountains to higher elevations, and occasionally found in Cabeza Prieta.

Native from Greece to Kashmir and southern Russia.

OP: N of Headquarters, 26 Mar 1965, *Ranzoni 310* (ORPI). Alamo Canyon, near old corral, 16 Feb 1979, *Bowers 1558*. Aguajita, 6 Apr 1988, *Felger 88-301*. 3.5 mi S of N boundary of Monument, Hwy 85, 20 Feb 1988, *Felger 88-02*. Bates Well, 11 Mar 2003, *Felger 03-297*. Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger 05-295*

CP: Kino Peak Quad, UTM 3564500N 318050E 12,1650 ft, base of Scarface Mt, off dirt road, by S-running arroyo, in coarse sand, *Autenreith 20 Mar 1992* (ASC).

Setaria – Bristlegrass

Ephemerals or perennials. Inflorescences of contracted panicles. Spikelets subtended by one or more persistent, scabrous bristles (the bristles represent reduced panicle branches or branchlets). Spikelets panicoid, detaching below the glumes, awnless, with 2 florets, the lower one sterile and reduced to a lemma similar to the upper glume, the fertile lemma firm and tightly grasping the fertile palea and grain (the spikelet thus appearing to have a single floret).

Setarias reach their desert limits in the flora area—they do not extend into the western areas of Cabeza Prieta or into the adjacent Gran Desierto of northwestern Sonora. Their absence in these drier regions is probably due to the lack of dependable summer rains.

1. Perennials, roots stout and coarse ..... **Setaria macrostachya**
1. Summer fall ephemerals, roots weakly developed.

2. Spikelets more or less oval in outline, widest at middle; fertile lemmas very finely rugulose (evenly textured with a fine, bead-like textured surface, the beads in rows)..... **Setaria grisebachii**
2. Spikelets diamond-shaped, widest below middle; fertile lemmas coarsely rugose with transverse wrinkles ..... **Setaria liebmannii**

Setaria grisebachii E. Fournier
Grisebach's bristlegrass; *zacate cola de zorra*

Summer-fall ephemerals, highly variable in size, superficially resembling *S. liebmannii*. Leaf blades scabrous or sparsely pubescent on both surfaces. Panicles cylindrical, loosely flowered, usually held well above the few leaves on relatively long, slender culms. Bristles 1 below each spikelet, with forward-pointing barbs. Spikelets 1.7–1.9 mm long, more or less oval in outline, widest at the middle; sterile paleas often present, varying in size from much less than to more than half as long as the spikelets (best seen at 30× magnification), or sterile paleas absent (both conditions may be found on the same plant); fertile lemmas very finely rugulose, with a granular or bead-like pattern.

Canyons and slopes in the Ajo and Diablo Mountains. More than a half dozen beautifully preserved florets as old as 20,500 years were recovered from fossil packrat middens in the Ajo Mountains.

This grass occurs in an arc around the northern and eastern limits of the Sonoran Desert, mostly at slightly higher elevations than the desert. Southwestern USA to Central America.

The texture of the fertile lemma needs to be inspected before being confident of distinguishing *Setaria grisebachii* from *S. liebmannii*. This is easily done by putting a drop of water on the spikelet and lifting the second glume and looking at the texture of the fertile lemma, using a 10× lens. The overall geographic ranges of the two species are similar except in the north where they tend to diverge.

OP: Mid-Alamo Canyon, bed of wash, 18 Dec 1945, *Goodding 474-45*. Arch Canyon, W of the arch, 2 Dec 1990, *Felger 90-551*. Trail to Mount Ajo, 3800 ft, 22 Oct 2006, *Rutman 2006-1022-9*. Diablo Mts, 807 m, shaded base of N-facing cliff, 22 Sep 2013, *Rutman 20130922-10* †Montezuma's Head, florets, 13,500 & 20,490 ybp.

Setaria liebmannii E. Fournier
Summer bristlegrass, Liebmann's bristlegrass; *zacate cola de zorra*. Figure 67.

Summer-fall ephemerals, highly variable in size, culms unbranched or with several or more slender branches. Leaf blades relatively broad, thin, yellowish green, and scabrous on both surfaces. Panicles cylindrical, loosely flowered, usually held well above the few leaves on relatively long, slender culms. Bristles 1 below each spikelet, with forward-pointing barbs. Spikelets 2.1–2.5 mm long, diamond-shaped, widest below the middle; sterile paleas absent; fertile lemmas coarsely rugose with transverse wrinkles.

Known in the flora area only from the Ajo Mountains.

This grass is mostly a tropical species and is the only annual bristlegrass in the lowland desert in Arizona and lowland desert and thornscrub in western Sonora and northwestern Sinaloa. Organ Pipe to central Arizona near the Mexican border, and Mexico to Central America.

Van Devender et al. (1990) reported this species from Montezuma's Head, 20,490 ybp, but the specimens apparently are *S. grisebachii* and not *S. liebmannii*.

OP: Alamo Canyon, on rocky slopes, *Goodding 25 Sep 1943*. Arch Canyon, shaded microsite below the arch, 2880 ft, 12 Sep 2013, *Rutman 20130912-19*.

Setaria macrostachya Kunth complex
Plains bristlegrass; *zacate tempranero*. Figure 68.

Tufted, often robust, perennial clumping grasses, with well-developed, strong, fibrous roots. (Sometimes flowering in the first season farther east in southern Arizona.) Panicles strongly contracted and spike-like, cylindrical, and densely flowered. Bristles solitary, with forward-pointing barbs. Spikelets 1–3 mm long, globose, the fertile lemmas coarsely rugose with transverse wrinkles. Flowering with sufficient soil moisture at various seasons, especially with summer-fall rains.

Figure 67. *Setaria liebmannii*. Arch Canyon. (A & B) 13 Sep 2013; (C) 22 Sep 2013.

Figure 68. *Setaria macrostachya*. (A) Plant, panicle and leaf blade, and spikelets (opened with glumes and sterile lemma, below; fertile lemma with palea spread open, middle; spikelet and bristle); (B & C) Alamo Canyon, 9 Sep 2013.

Locally common in scattered places in Organ Pipe except the more arid areas. Small arroyos and washes, canyons, and sandy loam to rocky slopes to higher elevations including the Ajo Mountains. Also canyons and mountain slopes in the eastern part of Cabeza Prieta westward to the Cabeza Prieta Mountains, especially at higher elevations. It has been in the Ajo Mountains for at least 32,000 years and was in Tinajas Altas more than 11,000 years ago. The specimens from Montezuma's Head, 13,500 ybp, are represented by several florets 2 mm long.

The *Setaria macrostachya* complex ranges from Colorado southward through much of Mexico. Part of this complex, including populations in southwestern Arizona and adjacent northwestern Mexico, has been segregated as *S. leucopila* (Scribner & Merrill) Schumann. McVaugh (1983: 361) noted that "after a little practice one can see the difference between the very plump fruit of the one and the less plump fruit of the other, the convexity or lack of it in the fertile palea, and the length of the sterile palea, can be diagnostic in the extremes, but not very useful in intermediate forms." In *S. leucopila* the fertile lemma is gibbous and in *S. macrostachya* sensu stricto it is not. Rominger (1962, 2003) distinguished *S. leucopila* also on the bases of leaf width, *S. leucopila* is supposed to have a narrower leaf. This distinction, however, does not hold up, leaf width seems to be a function of duration of rainfall and temperature (Felger & Wilder 2012, Felger et al. 2011).

OP: Alamo Canyon, *Nichol 4 May 1939*. Boulder Canyon, 2600 ft, 3 May 1978, *Bowers 1294*. Walls Well Rd, *Van Devender 30 Aug 1978*. 0.5 mi E of Lukeville, 11 Nov 1987, *Felger 87-313*. Mouth of Arch Canyon, 2 Dec 1990, *Felger 90-565*. About 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-4*. †Alamo Canyon, florets, 1150 to 32,000 ybp (7 samples). †Montezuma's Head, florets, florets, 13,500 to 21,840 ybp (3 samples). †Puerto Blanco Mts, florets, 2340 to 14,120 ybp (11 samples, Van Devender et al. 1990: 339).

CP: Agua Dulce Spring, 1400 ft, *Simmons 24 Jan 1965*. Canyon slopes at Agua Dulce Tank, 13 Jun 1992, *Felger 92-570*. Cabeza Prieta Tanks, 15 Jun 1992, *Felger* (observation).

TA: †Tinajas Altas Mts, florets, 10,950 ybp (Van Devender et al. 1990: 341).

***Sorghum halepense** (Linnaeus) Persoon
Johnson grass; *zacate Johnson*. Figure 69.

Figure 69. *Sorghum halepense*. (A) Plant, panicle, terminal spikelet cluster with paired pedicellate spikelets and the larger sessile, fertile spikelet, and an awnless fertile floret with a pair of pedicels; (B) Sedona, Yavapai Co., 25 Sep 2013, photo by Max Licher, from SEINet.

Perennials, potentially robust and to 1+ m tall, but probably much smaller in the flora area, with strong rhizomes in better-watered habitats, or facultative annuals without rhizomes. Growing and flowering with warm weather. Leaf blades 0.8–2+ cm wide, flat with a prominent midvein. Inflorescences of panicles, usually open, and breaking apart at maturity; branches not floriferous to the base. Spikelets andropogonoid. Sessile maturity breaking, bisexual spikelets relatively slender, awnless or with once bent (geniculate), twisted, and readily deciduous awns often 7–13 mm long; awned and awnless spikelets sometimes on the same panicle. Pedicellate spikelets staminate smaller, elliptic, awnless, and deciduous at maturity.

Washes and drainageways in Organ Pipe near the international border east of Lukeville, spreading from the adjacent agricultural fields in Mexico, and one record from Childs Mountain. Occasionally found along roadsides.

Native to the Mediterranean, now in the warmer parts of the world. Grown as a forage and fodder crop but also considered a noxious weed.

OP. 1 mi E of Lukeville, 11 Nov 1987, *Felger 87-325*.
CP. Childs Mt, 2000 ft, *Simmons 30 Oct 1962* (CAB).

Sporobolus – Dropseed

Ephemerals or perennials of diverse sizes and growth habits. Ligules a line of hairs (ciliate), sometimes also with large hairs at the collar and leaf sheath "behind the collar." Inflorescences of strongly contracted to open panicles. Spikelets small, with 1 floret, glabrous, awnless, and separating above the glumes. Glumes different in size, or sometimes subequal. Lemmas 1-veined. Grain readily falling from spikelets at maturity (hence the name "dropseed"); pericarp usually thin and closely enclosing the seed but free from it, readily soaking up water, becoming mucilaginous when wet and forcibly ejecting the seed, the "naked" seed often clinging to the tip of the palea and lemma especially after a rain. Among the Sonoran Desert species, growth and flowering occur during the warmer times of the year. Key characters include a ciliate ligule, spikelets with 1 floret, and 1-veined lemmas.

Among the dropseed grasses in the flora area, the young panicles often are strongly contracted and partially to even fully enclosed in an enlarged leaf sheath, at least at first in *Sporobolus cryptandrus*, *S. flexuosus*, and *S. pyramidatus*, and the lower portion of the panicles are also often contracted in *S. airoides*. As the panicles mature the branches usually spread: the contrast is striking and can be confusing for identification. "Those species of *Sporobolus* in which some or all of the inflorescences remain enclosed in the subtending leaf sheaths tend to reproduce cleistogamously, that is, pollen cannot be dispersed and obligately pollinates the stigma of the same floret. The percentage of seed set in these inbred plants is usually quite high" (Yatskievych 1999: 727).

Sporobolus cryptandrus is part of a complex including *S. contractus* Hitchcock, *S. flexuosus*, and *S. giganteus* Nash. These species have conspicuous tufts of hair at the summit of the leaf sheath. *Sporobolus cryptandrus*, which often produces the smallest-sized plants, is the most common and widespread member of this complex in the Sonoran Desert region. Some specimens from Arizona (Tinajas Altas and Tule Well) and northwestern Sonora appear intermediate with *S. flexuosus* in having swollen pulvini with hairs but with relatively small and mostly contracted panicles characteristic of *S. cryptandrus* (Felger 2000). Patrick Alexander (pers. comm. to R. Felger 2014) points out that *S. cryptandrus* and *S. flexuosus* in New Mexico produce mostly or completely cleistogamous inflorescences in dry years, and the panicles remain enclosed in the leaf sheath, probably a means of ensuring seed set when conditions are poor. In wetter seasons or years the

inflorescences generally extend half way or more out of the sheath. Similar scenarios seem to hold for the Sonoran Desert.

1. Ephemerals; branches at lowest node of panicle whorled with (4) 5 or more branches (often concealed by the leaf sheath in younger inflorescences); spikelets 1.5–1.8 mm long ..... **Sporobolus pyramidatus**
1. Perennials; branches at lower nodes mostly solitary, rarely with 3 branches (lower nodes of young inflorescences often concealed by the leaf sheath); spikelets 1.8–2.4 mm long.

2. Large, coarse grasses, often reaching 1–1.5+ m tall; hairs at the collar region of leaf, if present, usually straight; larger (lower) branches of panicles 6.5 cm or more long; grain (seeds) 0.95–1.2 mm long ..... **Sporobolus airoides**
2. Medium-sized or slender and relatively delicate grasses, the culms slender, if culms and panicles more than 1 m long then usually tangled and growing through shrubs, otherwise usually less than 1 m; leaf collar with a dense and often tangled mat of hairs; grain (seeds) 0.7–0.9 mm long.

3. Plants erect-ascending and free-standing, usually not more than 0.75 m tall; pulvini not hardened into hooks, not as below; spikelets generally appressed to the branches ..... **Sporobolus cryptandrus**
3. Plants often reaching 1–1.6 m, the panicles long, lax, often curved and clambering into shrubs and sometimes becoming tangled; pulvini at base of panicle branches becoming hardened into persistent hooks, and with a few, rather stout hairs; spikelets generally spreading ..... **Sporobolus flexuosus**

Sporobolus airoides (Torrey) Torrey subsp. **airoides**
Alkali sacaton; *zacatón alcalino.* Figure 70.

Coarse perennials often 1–1.5 m tall, forming large clumps with tough, knotty bases and very well-developed roots. Sometimes forming clonal "fairy rings" to 2+ m wide. Leaves mostly basal, the blades coarse and tough, often (30) 50–85 cm long; leaf sheaths sparsely pilose "inside" the summit of the leaf sheath, the collar region glabrous; lower portion of leaf sheaths near base of plants persistent, rather firm, shiny and smooth. Panicles openly branched at maturity, (15) 25–53 cm long; larger panicle branches (6) 7–16 (20) cm long; branches mostly solitary at each node (rarely 3 or 4 branches per node). Spikelets 1.8–2.2 mm long. Anthers 1–1.5 mm long. Grain (seeds) 0.95–1.2 mm long. Mostly growing April–November, dormant during the cooler months.

Locally common on alkaline flats, often in moist, sandy soil at Quitobaquito, Burro, and Williams Springs. Also found in the canyon bottom and water seeps at Cabeza Prieta Tanks.

Western USA and northern Mexico, often on alkaline or semi-saline soils. Another subspecies occurs in Coahuila.

OP: Quitobaquito, 9 Aug 1979, Bowers 1803. Williams Spring, 13 Sep 1986, *Felger 86-273*
CP: Cabeza Prieta Tanks, 15 Jun 1992, *Felger 92-604*

Sporobolus cryptandrus (Torrey) A. Gray
Sand dropseed; *zacate areñero.* Figure 71.

Tufted perennials, 30–75 (100) cm tall. Leaf sheaths usually pilose with relatively dense, long white and often tangled hairs at the summit, these hairs usually extending onto part of the collar. Base, or sometimes the entire panicle, enclosed by an enlarged, inflated leaf sheath (often with a reduced blade), the upper part of the panicle often but not always becoming free and the branchlets

Figure 70. *Sporobolus airoides*. (A) Plant, panicle, glumes, and two views of lemma and palea, (B & C) Quitobaquito, 13 Sep 2006.

spreading at maturity. Panicles (including enclosed portion) often 20–30 cm long, erect or arched, panicle branches single at nodes of exposed upper branches, often 3–5 (6) cm long. Spikelets 1.9–2.4 mm long, tan to dark olive-gray. Anthers 0.15–0.6 mm long. Grain (seeds) 0.7–0.9 mm long. Growing and reproductive during the warmer months.

Widely scattered in Organ Pipe and apparently scarce in Cabeza Prieta. Mostly along margins of washes, swales, and floodplains on sandy loams of the lower bajadas and valley floors, and infrequent on rocky slopes. Known from Tinajas Altas by single record.

Southern Canada to central Mexico.

OP: Quitobaquito, 24 Oct 1990, *Felger 90-474*. Tributary to Cuerda de Leña, 11 Sep 2013, *Rutman 20130912-10*. Diablo Mts, wash, along Ajo Mt Drive, 12 Sep 2013, *Rutman 20130912-10*
CP: Childs Mt, 2750 ft, 18 Aug 1992, *Felger 92-643d*. Tule Tanks, 30 Nov 1938, *Goodding A9590*.
TA: Tinajas Altas, 6 Dec 1935, *Goodding 599*

Figure 71. *Sporobolus cryptandrus*. (A) Plant, panicle, and spikelet with glumes separated from the floret, (B) Hwy 86, east of Why, Pima Co, 17 Sep 2013, (C) Cuerda de Lena, N boundary of Organ Pipe, 17 Sep 2013, (D) Hwy 86, east of Why, 12 Sep 2008.

Sporobolus flexuosus (Thurber ex Vasey) Rydberg
[*S. cryptandrus* var. *flexuosus* (Thurber ex Vasey) Thurber]
Mesa dropseed. Figure 72.

Tufted perennials similar to *Sporobolus cryptandrus*, semi-scandent, often reaching 1–1.6 m, with long, lacey, lax, and often curving panicles, sometimes somewhat prehensile in spiny shrubs. Panicles to 60 cm long, often drooping and loosely clambering into shrubs. Exposed panicle branches (parts not enclosed in the subtending leaf sheath; see *S. cryptandrus*) reaching 12–15 cm long, often spreading and becoming tangled. Pulvini at base of panicle branches swollen and with several stout hairs, hardening at maturity, the branches or branchlets falling away leaving the pulvini and a short portion of the branch as persistent hooks becoming tangled and anchoring the panicles onto shrubs. The distinctive pulvini often are seen only on mature panicles.

In the northern part of Organ Pipe and small scattered populations elsewhere in the Monument; sandy and sandy-loam soils of drainage channels, swales, and floodplains.

Northern Mexico and southwestern USA.

OP: E of Armenta at 2.2 mi W of Hwy 85, *Wirt 8 Sep 1990*. Sonoyta Valley, 0.4 mi E of Boundary Monument 164, *Rutman 29 Aug 2001* (ORPI). 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-12*

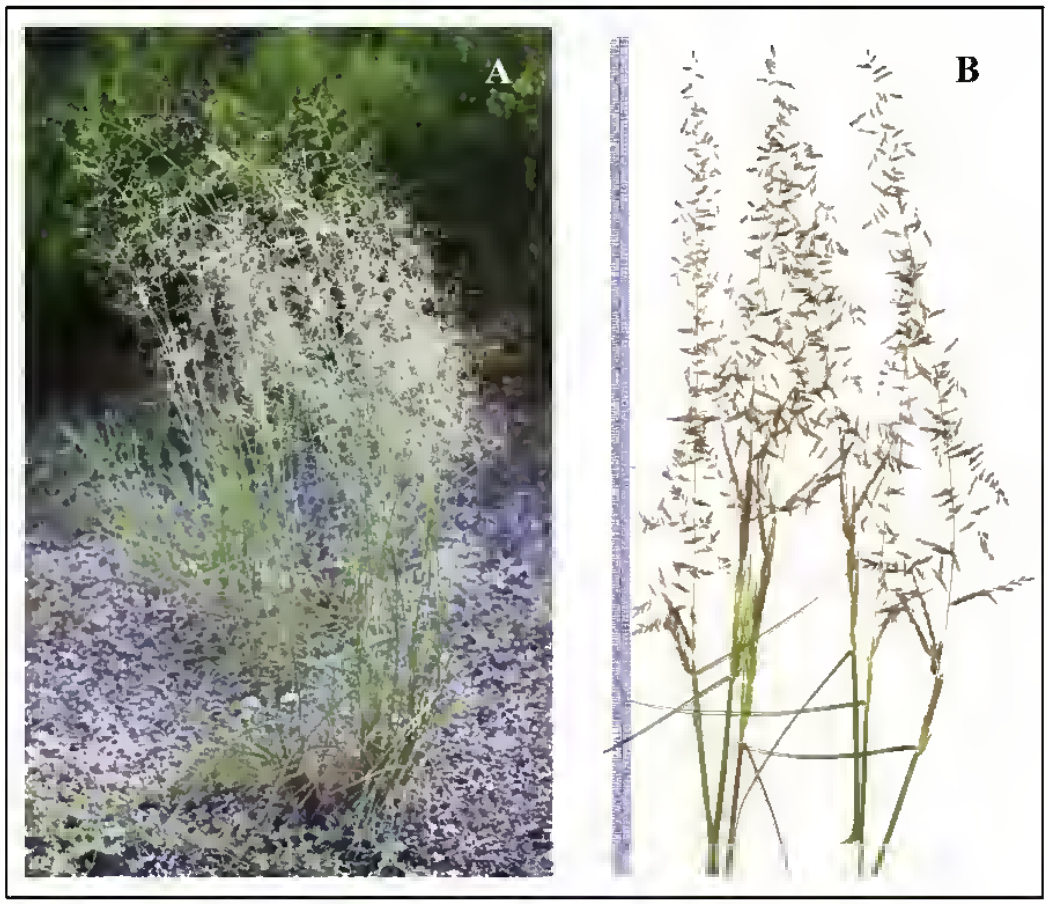

Figure 72. *Sporobolus flexuosus*. (A) Why, Pima Co., 21 Sep 2012; (B) sandy wash near N boundary of Organ Pipe, west of Hwy 85, 15 Sep 2013.

Sporobolus pyramidatus (Lamarck) Hitchcock
[*S. patens* Swallen. S. *pulvinatus* Swallen]
Whorled dropseed

Hot-weather ephemerals in the Sonoran Desert (elsewhere often perennials), highly variable in size, erect to spreading, often 10–25+ cm tall. Upper margin of leaf sheaths sparsely pubescent with long white hairs (not in dense tufts). Panicles at first contracted and narrow, often partly enclosed by the leaf sheath, the branchlets ultimately spreading and the panicles somewhat pyramidal. Lower panicle branchlets whorled, (4) 5–11 per node; upper panicle branchlets single at nodes; branchlets very slender with glandular areas appearing as lighter-colored, elliptic depressions or patches, and may be sticky. (These glands, seen with magnification, may be cryptic and their extent variable.) Spikelets 1.5–1.8 mm long. Lower glume much smaller than the upper one. Anthers 0.3–0.4 mm long. Grain (seed) 0.8–0.9 mm long.

Seasonally abundant in the springs of the Quitobaquito Hills, especially in floodplains of washes and margins of small watercourses, spring slopes, along irrigation ditches in the old fields and moist soil of alkaline flats.

Southern and Midwestern USA to Argentina.

OP. Williams Spring, *Van Devender 30 Aug 1978*. Aguajita, 14 Sep 1988, *Felger 88-420*.

Tridentopsis
[*Tridens*, in part]

Tufted perennials with hard, knotty bases. Culms nodes pubescent. Panicles slender and raceme-like or openly branched. Spikelets laterally compressed, breaking apart above the glumes and between the florets, and with multiple florets (5–12 in the flora area), the uppermost florets reduced and sterile. Glumes 1–7 veined. Lemmas prominently 3-veined, the tips rounded or minutely notched. Anthers reddish purple. *Tridentopsis* includes at least two species in western North America (Peterson et al. 2014).

1. Ligules glabrous; panicles open and spreading, usually more than 10 cm wide; spikelets 3–5 (7) mm long ..... **Tridentopsis eragrostoides**
1. Ligules hairy; panicles strongly contracted (narrow), often spike-like, to 1 (1.5) cm wide; spikelets 9–13 mm long ..... **Tridentopsis mutica**

Tridentopsis eragrostoides (Vasey & Scribner) P.M. Peterson
[*Tridens eragrostoides* (Vasey & Scribner) Nash]
Lovegrass tridens

Tufted perennials to nearly 1 m tall with slender culms and panicle branches. Culm nodes sparsely pubescent. Ligules glabrous. Panicles often more than 20 cm long and nearly as wide, open and lacey with slender branches. Spikelets often about 5 mm long with 5–10+ florets. Lemmas and sometimes the glumes with a delicate awn or bristle (mucro) less than 0.5 mm long, or awnless.

Poorly known in the flora area; in the Ajo Mountains, generally at higher elevations, especially north-facing slopes.

Organ Pipe and eastward in southern Arizona. Southern USA to Venezuela, and the Caribbean.

OP. W side Alamo Canyon, 13 Sep 1941, *Goodding 295-41*. Arch Canyon, N-facing slopes, 900 m, desertscrub with lowermost *Vauquelinia, Rhamnus betulifolia, Juniperus*, 2 Dec 1990, *Felger 90-539*.

Tridentopsis mutica (Torrey) P. M. Peterson var. **mutica**
[*Tridens muticus* (Torrey) Nash var. *muticus*]
Slim tridens. Figure 73.

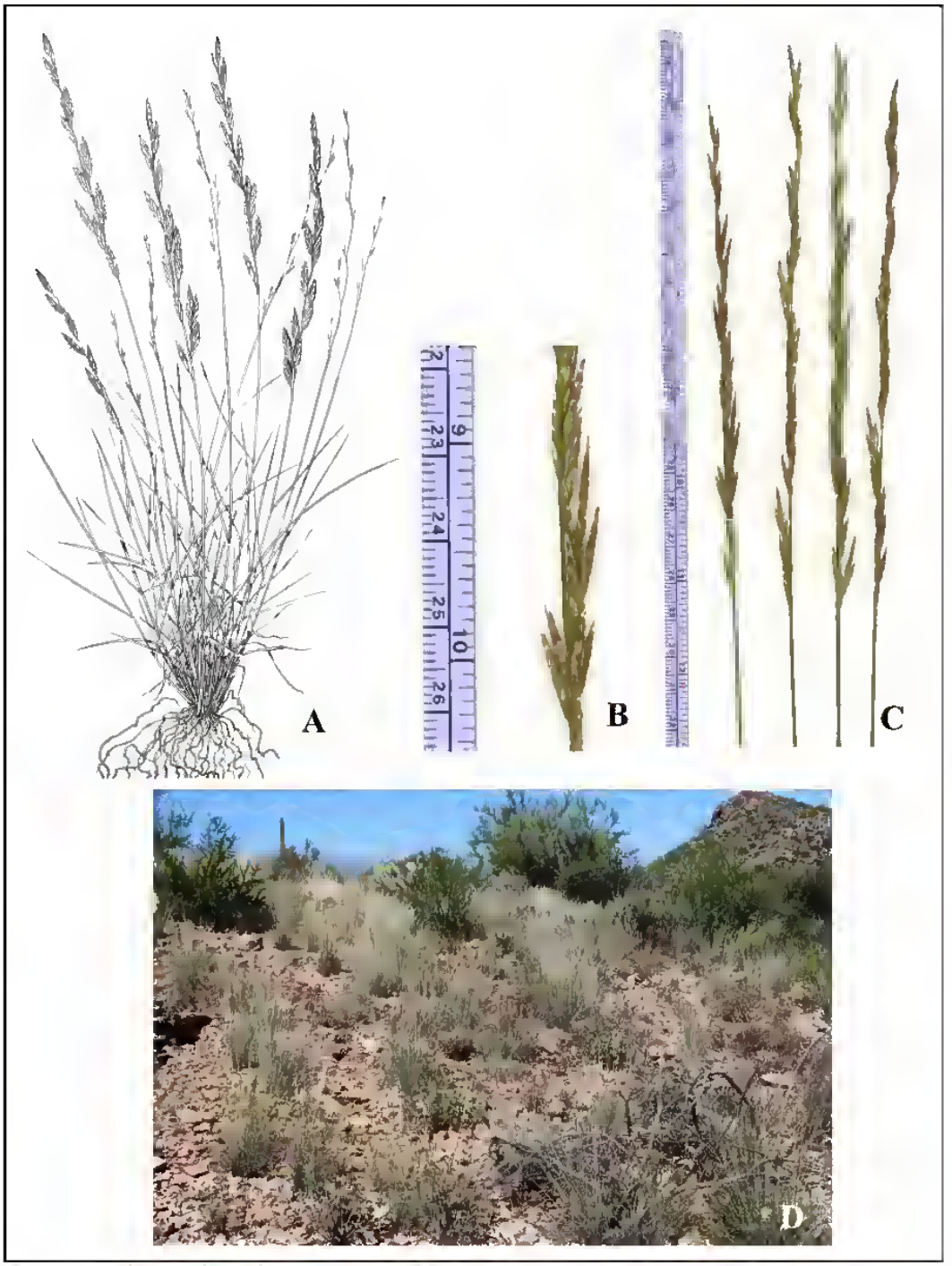

Figure 73. *Tridentopsis mutica*. (A) Plant Diablo Mts, west of Boulder Canyon, 22 Sep 2013 (B & C) panicles, (D) a dense stand

Tufted perennials (22) 28–40 (50) cm tall, with firm, slender culms. Leaves often bluish glaucous. Collar and ligule with a dense tuft of long white hairs, the sheaths sparsely to moderately pubescent with similar hairs; leaf blades slender and usually tightly inrolled. Growth and flowering response apparently non-seasonal. Panicles slender and spike-like, with closely appressed short branches, each branch with 1–several spikelets. Spikelets (5.5) 6.5–13.5 mm long, awnless (or lemmas sometimes with a minute awn or mucro). Glumes persistent, shorter than the spikelets. Florets strongly overlapping. Lemmas (3) 3.5–5.2 mm long, the lower parts (about the lower half) with densely hairy (pilose) veins. Spikelets green during hot and often humid weather of summer and early fall, and purplish at other seasons.

Common across the region, mostly on rocky slopes, canyons, and arroyos with shallow soils; hills and mountains often to the peaks. One of the most widespread and drought-tolerant perennial grasses in the region and often in surprisingly harsh, xeric habitats such as the hyperarid Sierra del Rosario in the Gran Desierto of Sonora, south of the Tinajas Altas region (Felger 2000). The single fossil record in the region, from the Ajo Mountains, is about 1200 years old.

Two varieties are often recognized. Variety *mutica* occurs in southwestern USA and northern Mexico and typically grows on rocky, or firm substrates. Variety *elongata* does not occur in the Sonoran Desert and ranges into higher elevations, extending farther eastward and northward in the USA than does var. *mutica*. Some authors, however, treat var. *elongata* as a synonym of var. *mutica* or recognize it as a distinct species.

OP: Bates Well, *Nichol 26 Apr 1939*. Alamo Canyon, 2500 ft, 16 Feb 1979, *Bowers 1559*. Twin Peaks, above Park Service residence area, 9 Sep 1984, *Van Devender 84-448*. Quitobaquito, 29 Mar 1988, *Felger 88-117*. †Alamo Canyon, 1150 ybp.

CP: Charlie Bell Pass, 3 Apr 1992, *Whipple 3955*. *Felger*, observations: Childs Mt, 18 Aug 1992; Sheep Mt, N side, mid-elevations to peak, 31 Jan 1992, Eagle Tank, Granite Pass Tank, 12 & 13 Jun 1992. Tule Mts, near crestline, *Rutman 17 Feb 2002*. Sierra Pinta, summit, *Cain 15 Nov 2003*.

TA: Borrego Canyon, 16 Jun 1992, *Felger* (observation). Tinajas Altas Mts, 26 Oct 2004, *Felger 04-75*.

****Triticum aestivum** Linnaeus

Wheat, common wheat; *trigo*; pilkañ. Figure 74.

Cool season ephemerals with large spikes bearing stout, bristly awns 7–15+ cm long. Wheat plants are occasionally seen along highways in nearby Sonora growing from grain spilled from passing trucks, and occasional plants are seen in Organ Pipe, especially along roads. Sterile wheat was used in a roadside seeding in Organ Pipe in 2005.

Native to the Old World. Widely cultivated in Sonora and Arizona.

OP: International boundary just W of Senita Basin, *Rutman 29 May 1998* (ORPI). Sand along road to Pozo Nuevo 1 mi N of international boundary, single plant, *Rutman 12 Mar 2001* (ORPI). Hwy 85, roadside seeding, N of park headquarters, area of roadside construction [see note for *Polypogon monspeliensis*], 9 Apr 2005, *Felger 05-159*.

Figure 74. *Triticum aestivum*. Hwy 85 roadside, Organ Pipe: (A) 9 Apr 2003; (B) 18 Jan 2006.

Urochloa arizonica (Scribner & Merrill) Morrone & Zuloaga
[*Panicum arizonicum* Scribner & Merrill. *Brachiaria arizonica* (Scribner & Merrill) S.T. Blake]
Arizona signal-grass; *piojillo de Arizona*. Figure 75.

Hot-weather ephemerals, slender and single-stemmed to sometimes many branched, light green and variously soft-pubescent, the hairs often bulbous-based, or the culms and leaves sometimes glabrous or essentially so. Roots weakly to well developed. Leaf size and width varying with soil moisture and warmth. Inflorescences of panicles 9–16 cm long with spike-like branches, the branches triangular in cross-section. Panicle branches and pedicels conspicuously hairy, the hairs often bulbous-based. Pedicels shorter than the spikelets. Spikelets panicoid, breaking off below the glumes. Spikelets generally elliptic, 2.8–3.8 mm long, mostly hairy but sometimes glabrous, pale green or reddish, the upper glumes and sterile lemmas with longitudinal veins and a net-like pattern of green cross-veins toward the tip, or cross veins sometimes absent. Lower glume often to about half as long as the spikelet. Lower floret sterile or staminate, with a lemma and palea, the lemma similar to upper glume. Fertile lemma hard, the margins inrolled, enclosing the palea and grain.

Washes, arroyos, sand flats, and canyons; widespread and seasonally common across much of Organ Pipe except the most arid areas, and Cabeza Prieta from the Pinta Sands eastward.

Texas to southern California and southward to Oaxaca.

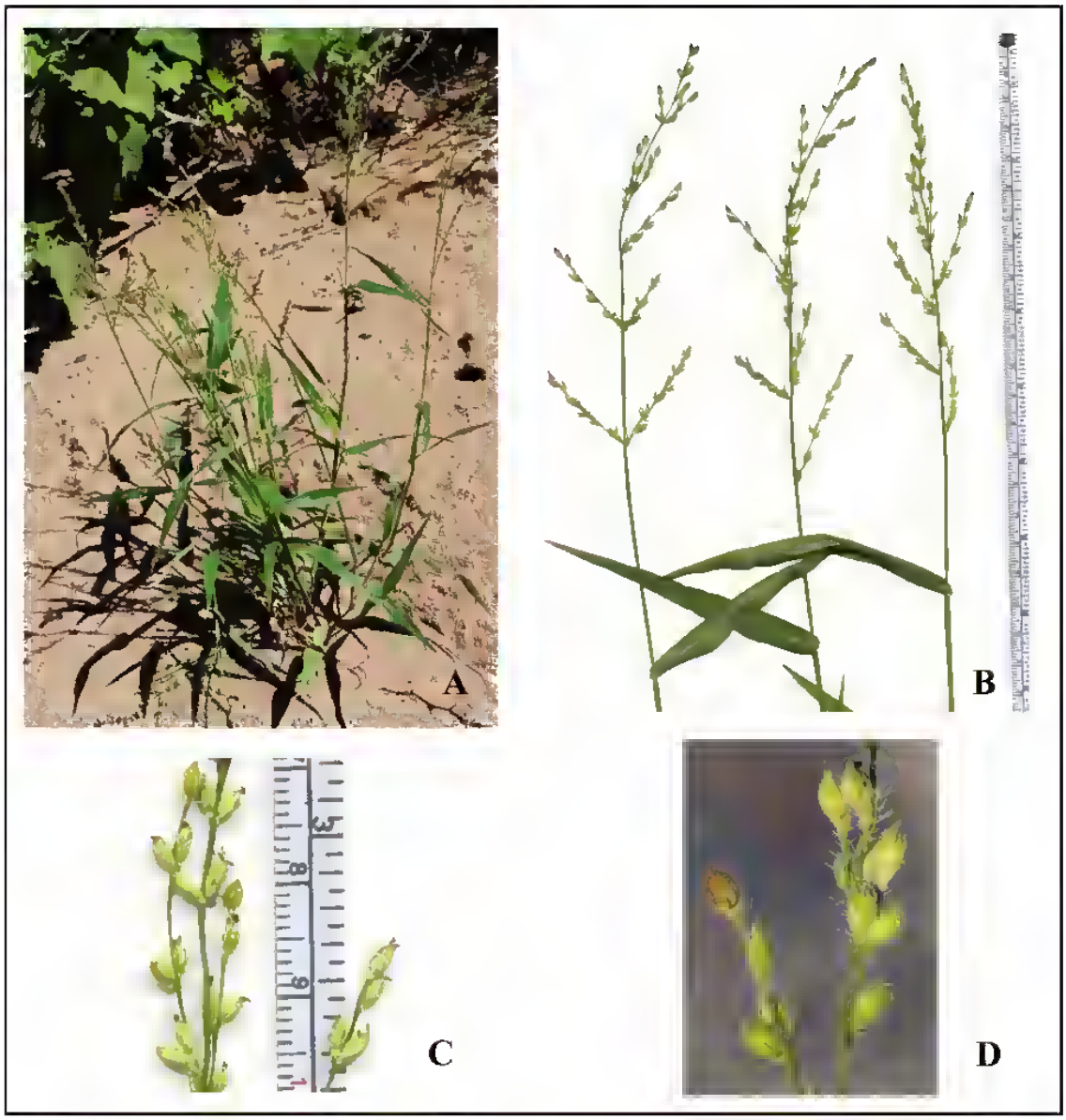

Figure 75. *Urochloa arizonica*. (A) Alamo Canyon, 15 Sep 2013; (B) between Armenta Ranch and Hwy 85, 6 Oct 2012, (C & D) Hwy 85, near N boundary of Organ Pipe, 11 Sep 2008

OP: Sonoyta Hills, sandy flats along arroyo, 27 Aug 1943, *Clark 10891* (ORPI). 8 mi by road W of Visitor Center along Puerto Blanco Drive, 16 Oct 1977, *Bowers 894*. Armenta Well Ranch, 13 Sep 1978, *Bowers 1532*. Estes Canyon, 12 Sep 1978, *Bowers 1519*. 1.5 mi W of State Route 85 and 0.15 mi S of Armenta Ranch Road, 30 Sep 2006, *Rutman 20060930-13*.

CP: East Pinta Sands, 15 Sep 1992, *Felger 92-759*. Arroyos along Charlie Bell Rd, 18 Aug 1992, *Felger* (observation). Road from Bates Well to Papago Well, 1.7 mi SW of W boundary of Organ Pipe, 14 Sep 1992, *Felger 92-698*

Vulpia, see **Festuca**

††**Zuloagaea bulbosa** (Kunth) Bess
[*Panicum bulbosum* Kunth. *P. plenum* Hitchcock & Chase]
Bulb panic grass

Perennials often 50+ cm tall, with short, knotty rhizomes, the culm bases swollen and bulbous, forming an ovoid corm—a unique feature among the grasses of the region. Spikelets panicoid, 3.5–4 mm long. A monotypic genus segregated from *Panicum*.

Zuloagaea bulbosa was in the Ajo Mountains during the last Ice Age. The nearest known present-day population is in the Baboquivari Mountains.

Widespread in Arizona above the desert, and not in the arid southwestern part of the state since the last Ice Age. Arizona to Texas and South America.

OP: †Alamo Canyon, florets, 14,500 to 32,000 ybp (3 samples)

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NEOTYPIFICATION OF *TRIFOLIUM PSORALIOIDES* WALTER (FABACEAE) AND ITS TRANSFER TO *ORBEXILUM*

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ABSTRACT

Trifolium psoralioides was described by Walter in 1788 in his *Flora Caroliniana*. This taxon has been treated as a member of several genera, including *Lotodes*, *Melilotus*, and *Psoralea*. The name now belongs in *Orbexilum*. A nomenclatural history of the eastern USA coastal plain taxon is presented, as well as a history of how the name has been applied in floras. A case is made for the need to transfer the name to *Orbexilum*, the combination is proposed, and a neotype is established for the name.

Thomas Walter (?1740–1789), an English planter and merchant, lived in what is now Berkeley County, South Carolina, on a plantation along the banks of the Santee River (Rembert 1980). Walter (1788) authored the first flora in North America based on the Linnean System, the *Flora Caroliniana*. In this book, Walter coined 414 names for plants he thought to be new (Ward 2007a). Specimens in a folio housed at the Natural History Museum, London (BM), donated by the family of John Fraser to that institution have long been called the "Walter Herbarium," and, indeed, some specimens bear names in the hand of Thomas Walter. Some specimens from this folio have been designated lectotypes or neotypes for some of Walter's names (see, for example, designations by Fernald & Schubert 1948 and Ward 2007a, b, c, d, e, f). Ward (2007c) indicated that the "Walter Herbarium" is better called the "Fraser Herbarium," since it appears that specimens contained therein were likely collected by John Fraser. Other names published in the *Flora Caroliniana* are not represented by specimens (or adequate specimens) in that folio and have been neotypified (or epitypified) by other specimens (see Ward 2007b, d).

One name published by Walter in *Flora Caroliniana*, *Trifolium psoralioides*, is not typified by a specimen. The name has been applied in different ways by different authors (Table 1), and this has led to confusion about how the name should be applied (see Table 2 for ways in which this entity has been treated since 1788). The species has long been considered a member of the genus *Psoralea* and is now considered to belong in *Orbexilum*. At the rank of species, it has been considered by some authors as a synonym of *Psoralea pedunculata* (Mill.) Vail (basionym = *Hedysarum pedunculatum* Mill. 1768) or *Orbexilum pedunculatum* (Mill.) Rydb. If considered in this way, there are no nomenclatural problems resulting from the lack of a type specimen. At the rank of variety, the taxon would be a synonym of *Psoralea melilotoides* var. *gracilis* Torr. & A. Gray (1838), and again, no problems result from lack of a type if it is treated in this way. However, some authors have treated the eastern coastal plain entity as a separate species from the inland entity (Cory 1938; Rydberg 1919; Turner 2008). Indeed, there is evidence from both morphology (densely glandular calyces, bracts, and fruits, and other traits) and molecular data (Egan & Crandall 2008) to support recognition of the coastal plain entity as a separate species from the inland entity. If this is accepted, then typification of Walter's name becomes crucial, since it predates *Orbexilum gracile* (Torr. & A. Gray) Rydb. by over 130 years.

In his monograph of *Psoraleeae*, Grimes (1990) recognized two varieties of *Orbexilum pedunculatum*: var. *pedunculatum*, with abaxial leaflet surfaces, calyx tube, and fruits eglandular; and var. *gracile*, with abaxial leaflet surfaces, calyx tubes, and fruits glandular. In this monograph, Grimes lectotypified *Hedysarum pedunculatum* Mill. using a stem on a sheet in the Miller herbarium (BM) that matches the characters given above and stabilizes the Miller name. Grimes rejected *Trifolium psoralioides* as being ambiguous. However, this does nothing to truly deal with that name, which now becomes important. I believe that neotypifying the Walter name is the most parsimonious approach and brings the most nomenclatural stability to a very complex situation.

In order to determine an appropriate specimen to serve as a new type specimen, it is important to consider several points:

1. Thomas Walter did not designate type specimens for his taxa.
2. Walter's original material (if any) is mostly lost, though perhaps a small number of specimens he actually examined still exist in the "Walter/Fraser Herbarium" folio at BM (and photos of them at GH).
3. Walter did not stray far from home during the time he lived in the Carolinas (perhaps no more than 50 miles (Walter 1788).
4. The taxon now called "*gracile*" is the only one (at least now) native to the region in which Walter lived.
5. Walter's brief protolog is consistent with a description of the entity now called "*gracile*."

It seems obvious, to me at least, that *Trifolium psoralioides* Walt. is the same taxon as *Orbexilum pedunculatum* var. *gracile*. Therefore, in order to stabilize the nomenclature of the eastern USA coastal plain species of *Orbexilum*, a new combination is proposed here, with designation of a neotype.

Orbexilum psoralioides (Walt.) Vincent, **comb. nov.** *Trifolium psoralioides* Walt., Fl. Carol. 184. 1788. *Melilotus psoralioides* (Walt.) Nutt., Gen. N. Amer. Pl. 2: 104–105. 1818. *Lotodes psoralioides* (Walt.) Kuntze, Revis. Gen. Pl. 1: 194. 1891. *Orbexilum pedunculatum* var. *psoralioides* (Walt.) Isely, Sida 13(1): 122. 1988. *Psoralea melilotoides* Michx. (*nom. superfl.*), Fl. Bor.-Amer. 2: 58. 1803. *Psoralea psoralioides* (Walt.) Cory, Rhodora 38(455): 406. 1936. **NEOTYPE** (designated here): **South Carolina**. Berkeley Co.: Francis Marion National Forest, 3.47 airmiles ESE of Honey Hill, 7 Jun 2012, *J.B. Nelson 30632 with E. Kauffman* (USCH 112017). Figure 1.

Orbexilum pedunculatum var. *gracile* (Torr. & A. Gray) J.W. Grimes, Mem. New York Bot. Gard. 61: 47. 1990. *Psoralea melilotoides* (Michx.) Torr. & A. Gray ß *gracilis* Torr. & A. Gray, Fl. N. Amer. 1(2): 303. 1838. *Orbexilum gracile* (Torr. & A. Gray) Rydb., N. Amer. Fl. 24(1): 7. 1919. *Orbexilum gracile* (Torr. & A. Gray) B.L. Turner (*nom. illeg.*), Lundellia 11: 2. 2008. *Psoralea psoralioides* var. *gracilis* (Torr. & A. Gray) F.L. Freeman, Rhodora 39(467): 427. 1937. **TYPE**: "Pine woods, Middle Florida, *s.d., Dr. Chapman s.n.* (holotype: NY ![electronic image]).

Figure 1 Neotype specimen of *Trifolium psoralioides* Walt., *Nelson 30632* (USCH)

Table 1. Nomenclatural history of the coastal plain glandular *Orbexilum*

Author	Date	Name
Walter	1788	*Trifolium psoralioides* Walt.
Michaux	1803	*Psoralea melilotoides* Michx.[1]
Nuttall	1818	*Melilotus psoralioides* (Walt.) Nutt.
Torrey & Gray	1838	*Psoralea melilotoides* (Michx.) Torr. & A. Gray ß *gracilis* Torr. & A. Gray[2]
Torrey & Gray	1838	*Psoralea gracilis* Chapm. ex Torr. & A. Gray[3]
Kuntze	1891	*Lotodes psoralioides* (Walt.) Kuntze[4]
Vail	1894	*Psoralea pedunculata* (Mill.) Vail
Rydberg	1919	*Orbexilum gracile* (Torr. & A. Gray) Rydb.[5]
Cory	1936	*Psoralea psoralioides* (Walt.) Cory
Freeman	1937	*Psoralea psoralioides* (Walt.) Cory var. *typica* Freeman[6]
Freeman	1937	*Psoralea psoralioides* var. *gracilis* (Torr. & A. Gray) Freeman
Isely	1986	synonymized *T. psoralioides* with *Orbexilum pedunculatum* var. *pedunculatum*
Isely	1988	*Orbexilum pedunculatum* var. *psoralioides* (Walt.) Isely[7]
Grimes	1990	*Orbexilum pedunculatum* var. *gracile* (Torr. & A. Gray) Grimes
Turner	2008	*Orbexilum gracile* (Torr. & A. Gray) B.L. Turner[8]

[1] *nom. superfl.* (cites *Trifolium psoralioides* Walt. in synonymy)
[2] attributed to Chapman, based on an unpublished manuscript name
[3] *nom. nud.*
[4] as "psoralodes"
[5] as "(Chapm.) Rydb."
[6] *nom. illeg.*, ICBN Art. 24.3
[7] as "(Chapm.) Isely", but Isely gives the correct basionym and author
[8] invalid; isonym

Table 2. Historical treatment of coastal glandular *Orbexilum* in floras

Author	Date	Treated as:	*psoralioides* mentioned?
Elliott	1824	*Psoralea melilotoides*	as synonym
Gray	1887	*Psoralea melilotoides*	no
Britton & Brown	1897	*Psoralea pedunculata*	no
Small	1903	*Psoralea gracilis*	no
Robinson & Fernald	1908	*Psoralea pedunculata*	no
Small	1913	*Psoralea gracilis*	no
Small	1933	*Orbexilum gracile*	no
Massey	1961	*Psoralea psoralioides*	
Wilbur	1963	*Psoralea psoralioides* var. *psoralioides*	
Radford et al.	1964	*Psoralea psoralioides* var. *psoralioides*	
Harvill	1970	*Psoralea psoralioides*	
Duncan & Kartesz	1981	*Psoralea psoralioides* var. *psoralioides* and var. *gracilis*	
Isely	1990	*Orbexilum pedunculatum* var. *gracile*	yes
Gleason & Cronquist	1991	*Orbexilum pedunculatum* var. *gracile*	yes
Harvill et al.	1992	*Psoralea psoralioides*	
Isely	1998	*Orbexilum pedunculatum* var. *gracile*	yes
Wunderlin	1998	*Orbexilum pedunculatum*	yes
Weakley et al.	2012	*Orbexilum pedunculatum* var. *psoralioides*	

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NEW SPECIES OF *BEGONIA* (BEGONIACEAE) FROM MEXICO AND CENTRAL AMERICA

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ABSTRACT

Begonia boqueronensis Burt-Utley & Utley and **B. calzadae** Burt-Utley & Utley from Chiapas, México, and **B. skutchii** Burt-Utley & Utley from Costa Rica are described as new, illustrated, and compared to relevant species recognized in the forthcoming volume of Flora Mesoamericana.

During preparation of the Begoniaceae for Flora Mesoamericana, several new species were previously described (Burt-Utley & Utley 2011, 2012), resulting in the recognition of 102 species in the preliminary manuscript of the Begoniaceae for the Flora. Two of the new species described herein, *B. boqueronensis* and *B. calzadae*, are placed in sect. *Gireoudia* (Kl.) A. DC. because of their apetalous flowers and trilocular ovaries, while the third has the fleshy bilocular ovaries characteristic of sect. *Weilbachia* (Kl. & Oerst.)A. DC. With these species, there are now 105 *Begonia* species know to occur within the boundaries of the Flora.

1. BEGONIA BOQUERONENSIS Burt-Utley & Utley, **sp. nov. TYPE. MÉXICO. Chiapas.** 1.5 km SW of Ojo de Agua along road from El Rosario to Niquivil, 1675 m, 6 Nov 1986, *D.E. Breedlove 65663* (holotype, CAS). Figure 1.

Begonia boqueronensis shares a number of characters with another species in the sect. *Gireoudia*, *B. strigillosa* A. Dietr., but is readily distinguished from this latter taxon by its rhizomes with often elongate internodes [(0.4–)2–3 cm vs. 0.3–0.8(–1.4 cm)] and its deciduous, narrowly ovate-triangular stipules vs the persistent broadly ovate to triangular stipules of *B. strigillosa* [8–17 x 4–8 mm vs. 10–19(–22) x 5–9 mm]. The lowermost obovate inflorescence bracts of *B. boqueronensis* are significantly smaller than the ovate to elliptic bracts of *B. strigillosa* (4.5 x 2 mm vs. 11–21 x 7–9 mm). Moreover, capsules of *B. boqueronensis* are smaller than those of *B. strigillosa* [0.8–0.9 cm vs 0.9–1.4(–2) cm].

Rhizomatous herbs to 21.5+ cm long; internodes short to elongate, (0.4–)2–4.5 cm, 1.5–3(–5) mm diam, squamose with broad laciniate scales to 4 mm throughout, cystospheres present. **Leaf blades** oblique, asymmetrically elliptic to ovate or obovate, (2.9–)4.8–14.8 x (1.9–)3.3–9.2 cm, basally cordate, apically acuminate, marginally ciliate and dentate to denticulate, crenulate or serrulate, sometimes with a shallow dentate lobe opposite the petiole insertion, above glabrous except for villi occasionally above the petiole-blade insertion, sparingly villous to squamose below on major nerves, intercostal regions glabrous, green above, often with maroon maculations, green or maroon throughout beneath; 9–11-palmatinerved; petioles (3–)6–12.7 cm, densely squamose with broad to narrow lacerate scales 2–5 mm and occasionally villi intermixed, cystospheres present; stipules deciduous, reflexed with age, narrowly ovate-triangular, 8–17 x 4–8 mm, marginally entire, revolute, glabrous to villous or the conspicuous keel only villous to squamose, cystospheres present. **Inflorescences** asymmetrically cymose, apparently greatly exceeding the foliage; peduncles 10–39 cm, sparingly villous and squamose; bracts caducous, the lowermost appearing obovate, 4.5 x 2 mm, marginally entire, glabrous. **Staminate flowers** with pedicels 1–2.7 cm, glabrous; sepals 2, elliptic to broadly ovate or suborbicular, 8–13.5 x 7–12 mm, glabrous, white to dark pink; petals wanting;

Figure 1. *Begonia boqueronensis*, holotype (*Breedlove 65663*, CAS).

stamens (6–)8–14, on a slightly raised torus or appearing free; filaments 1–1.5 mm, anthers oblong to obovate in outline, 1.3–1.7 x 0.7–0.9 mm. **Pistillate flowers** with pedicels 5–7 mm, glabrous; bracteoles wanting; sepals obovate to transversely elliptic, 6–8.5 x 6–9.5 mm, glabrous, white to dark pink, very sparingly glandular; petals wanting; ovaries trilocular with bipartite placentae, ovuliferous throughout, 4.5–8.5 mm, glabrous to very sparingly glandular, pink and sometimes maculate; styles 3, 2–3.5 mm, connate to ½ their length; stigmas lunate. **Capsules** with pedicels 7–14 mm; bodies 8–9 mm, locule chambers externally appearing ovate to ovate-elliptic, 6.5–9 x 4.5-6.5 mm; wings 3, unequal, the largest oblique, asymmetrically triangular to asymmetrically ovate, 6–10 x 8–9 mm, rounded to acute, occasionally denticulate distally, the second asymmetrically triangular, 4–6.5 x 5–8 mm, the third equal to subequal to the second or shallowly asymmetrically triangular to lunate.

Etymology. *Begonia boqueronensis* is named after Cerro Boquerón, where Purpus first collected this species.

Distribution and habitat. Slopes and ravines with *Pinus*, *Quercus*, and *Ostrya* between 1675 and 2255 m in southeastern Chiapas and Guatemala.

Begonia boqueronensis is distinguished from the apparent Chiapan endemic, *B. cristobalensis* Ziesenh., by a number of characters, including its often elongate, squamose internodes, in contrast to the short internodes of *B. cristobalensis* with its pubescence restricted to a ring scales at the bases of the petioles and its longer stipules [8–17 mm vs. 4–8(–10) mm]. When the number of nerves on leaf blades are compared, blades of *B. boqueronensis* are 9–11-nerved, while those of *B. cristobalensis* are 6–9-nerved. Comparing petiolar induments of these two species, the indument of *B. boqueronensis* consists of narrow to broad lacerate scales 2–5 mm long with occasional villi intermixed. In contrast, the indument of *B. cristobalensis* is villous throughout or villous with narrow scales 2–6 mm intermixed.

Specimens examined. MÉXICO. Chiapas. Ridge NE of Cerro Boquerón on rd from El Rosario to Niquivil, 2255 m, 29 Nov 1985, *Breedlove and Sigg 66051* (CAS); Cerro del Boquerón, Sep 1913, *Purpus 6932* (UC). **GUATEMALA. Quetzaltenango.** Region of las Nubes, S of San Martín Chile Verde, ca. 2250 m, 27 Jan 1941, *Standley 85183* (F).

2. BEGONIA CALZADAE Burt-Utley and Utley, **sp. nov. TYPE. MÉXICO. Chiapas.** Entre Finca Prusia y Triunfo, Sierra Madre, 1000–1300 m, 12 Jan 1971, *E. Matuda 38243* (holotype, MO; isotypes, CAS-2). Figure 2.

Begonia calzadae stands apart from other species in sect. *Gireoudia* in its often elongate lowermost inflorescence branches, also unusual are its lowermost staminate pedicels that can reach 9.5 cm in the Matuda collections (however, pedicel length in an inflorescence of *B. calzadae* decreases from the lowermost branches to the upper branches). *Begonia calzadae* can be distinguished from most other species of *Begonia* in Chiapas with squamose petioles by its short rhizome internodes.

Rhizomatous herbs; nodes with a ring of short but broad lacerate scales surrounding the bases of the petioles and stipules; internodes apparently short, 3.5–7 mm x 0.4–1.2 cm, glabrous, cystospheres present. **Leaf blades** oblique to rarely substraight, asymmetrically ovate to elliptic, 11.8–23.5 x 8–15.3 cm, apically abruptly short acuminate, basally cordate, marginally ciliate and shallowly dentate to denticulate at ends of major nerves; above with stout villi to 5 mm only above and near the petiole insertion, otherwise glabrous to minutely glandular, below squamose stoutly villous and glabrous to minutely glandular on major nerves, intercostal regions glabrous to minutely glandular with occasional villi occasionally present, abundant cystospheres at the base of nerves, leaves green throughout or with maroon maculations; 10–12-palmatinerved; petioles 12–33 cm, squamose, the broad lacerate scales 2–6 mm, spreading to reflexed, and a dense band of lacerate

Figure 2. *Begonia calzadae*, holotype (*Matuda et al. 38243*, MO).

scales 3–7 mm just below the petiole-blade junction, cystospheres abundant; stipules asymmetrically triangular, 1.2–2.3 cm x 7–8 mm, marginally somewhat revolute, entire, strongly keeled with the keel only sparingly villous to squamose, cystospheres present. **Inflorescences** dichotomously branched, but rarely trichotomous at the lowermost node, moderately asymmetric, often very many-flowered; peduncles 25–35 cm, glabrous to sparingly squamose; lowermost bracts wanting, the mid to upper bracts 9 x 6–7 mm, apically rounded to asymmetrically bilobed, marginally entire, sometimes weakly undulate, glabrous, often finely keeled especially distally. **Staminate flowers** with pedicels 1.1–5.5(–9.5) cm, glabrous to occasionally narrowly squamose; sepals 2, elliptic to suborbicular or obovate, (0.7–)1–1.6 x (0.5–)0.8–1.1 cm, glabrous to glandular, maroon maculate; petals wanting; stamens 8–12, appearing free or at least some on a very shallow torus; filaments 0.5–1.5 mm; anthers narrowly obovate, 1.5–2 x 0.7–1 mm. **Pistillate flowers** with pedicels 1.4–1.6 cm, occasionally villous distally; bracteoles wanting; sepals 2, suborbicular to broadly elliptic or transversely elliptic, 7–8.5 X 6.5–8 mm; petals wanting; ovaries trilocular with bipartite placentae, 7–9.5 mm, glandular and maculate; styles 3, 2 mm, fused half their length; stigmas lunate. **Capsules** with pedicels 1.1–1.7 cm; bodies 7-11 mm; locule chambers externally appearing ovate, 6–8 x 5–6.5 mm; wing 3, unequal, the largest asymmetrically triangular, 5–9.5 x 6–8 mm, apically rounded, acute or acuminate, the second asymmetrically triangular to lunate-triangular, 4–7 x 6.5–8 mm, apically acute to acuminate, the third asymmetrically lunate to lunate-triangular, 3–4.5 x 5.5–8 mm, apically rounded to subacute.

Etymology. *Begonia calzadae* is named in honor of J.I. Calzada, who collected this species from the same general area as Matuda's type.

Distribution and habitat. *Begonia calzadae* is known only from the region between El Triunfo and Finca Prusia in the Sierra Madre de Chiapas where it potentially ranges from 1200 m to 1600 m. Calzada's description of the location is this: "Bosque caducifolio ecotonía con Pinar, zona de cañadas, el suelo café orcilloso profundo."

Begonia calzadae is immediately distinguished from *B. boqueronensis* with its short internodes and from *B. cristobalensis* by its larger leaves (11.8–23.5 x 8–15.3 cm vs. 4.3-10 X 2.5-7 cm) and longer peduncles [(25–35 cm vs. 5.3–15.3(–16.3)] cm. *Begonia calzadae* also has a petiolar indument of broad lacerate scales 2–6 mm and an annulus of similar broad lacerate scales just beneath the blade insertion. In contrast, the petioles of *B. cristobalensis* are both villous or villous and squamose with villi and scattered narrow laciniate scales but no annulus. Leaf blades of *B. calzadae* also have more numerous nerves (10–12) than those of *B. cristobalensis* (6–9). When *B. calzadae* is compared with *B. hispidavillosa* Ziesenh., there is an obvious difference in stipule form and size, with those of *B. calzadae* appearing asymmetrically triangular and 1.2–2.3 cm x 7–8 mm vs. stipules of *B. hispidavillosa* that are asymmetrically very broadly ovate-triangular or hemiorbicular and 0.5–1.2 x 0.8–1.7 cm. Moreover, pedicels of both staminate and pistillate flowers of *B. calzadae* are typically much longer than those of *B. hispidavillosa* [♂ 1.1–5.5(–9.5) cm vs. 0.5–0.8(–1.2) cm; ♀ 1.4–1.6 cm vs. (2.5–)4.5–8 mm].

Specimens examined. MÉXICO. Chiapas. Mpio. Jaltenango de La Paz, senda de Campamento El Triunfo para Finca Prusia, 1600 m, 5 May 1988, *Calzada 14123* (MEXU, USF, XAL).

3. BEGONIA SKUTCHII Burt-Utley and Utley, **sp. nov. TYPE. COSTA RICA. San José.** 14.1 km W of square in San Isidro de El General in Fila Tinamastes along road to Dominical, ca 900 m, 27 Jun 1995, *K. Utley & J. Utley 9032* (holotype: USF; isotypes: CR, MO, US). Figure 3.

Begonia skutchii overlaps both *B. carletonii* Standl. and *B. turrialbae* Burt-Utley & Utley in a number of characters including internode lengths, leaf blade size and numbers of nerves. All three species

Figure 3. *Begonia skutchii*, holotype (*Utley & Utley* 9032, USF).

also have a petiolar indument with short villi. Stipules of *B. skutchii* are triangular to ovate, in contrast to those of *B. carletonii* that are often lance-triangular and more narrow (2–5 mm vs. 2–3 mm), while those of *B. turrialbae* are lance-ovate to lanceolate and similar in width to those of *B. skutchii*. Staminate sepals of *B. skutchii* are typically smaller than those of *B. turrialbae* [3–8(–11) x 2–4.5 mm vs. 6–17 x 4–12 mm] and generally more narrow than those of *B. carletonii* (2–4.5 mm vs. 3.5–6mm).

Rhizomatous herbs, the rhizomes elongate and branching; internodes short to elongate, slender, 0.5–4.5 cm x 1.2–3 mm, moderately to densely villous with trichomes 0.4–2 mm. **Leaf blades** substraight to oblique, asymmetric, ovate to oblong, 3.8–13.7 x 3.5–9 cm, basally cordate, apically attenuate-acuminate, marginally occasionally finely dentate or serrate, ciliate and glandular-ciliate-denticulate or serrulate, often with a broad rounded to acute lobe opposite the petiole insertion, above coarsely papillose and pustulate with villi 0.5–2 mm terminating some of the acuminate pustules, below finely alveolate and densely villous throughout with trichomes to 1 mm; (8–)9–11-palmatinerved; petioles 3.6–10.5(–15.5) cm, moderately to densely villous with trichomes 0.5–2 mm; stipules persistent to deciduous, triangular to ovate, (3–)5–9.5(–11) x (1.5–)2–5) mm, sparingly to densely villous. **Inflorescences** generally strongly asymmetrically cymose, when immature the branches and immature flowers strongly reflexed, few-many-flowered; peduncles (3.6–)6.2–15.3 cm, glandular and sparingly villous; bracts persistent to deciduous, oblong to oblong-ovate, 3–9 x 1–3 mm, glabrous to puberulous, pink. **Staminate flowers** with pedicels 5–19 mm, glandular and very sparingly short villous; sepals 2, elliptic to obovate, 3–8 (–11) x 2–4.5 mm, sparingly glandular and puberulous, internally white to pink, externally deep pink; petals 2, oblanceolate to narrowly elliptic, 2.5–6 x 1–2 mm, glabrous, white; stamens 13–25(–33), free or inserted on a low torus; filaments 0.4–0.7 mm; anthers oblong to obovate, 0.7–1.3 x 0.3–0.6 mm. **Pistillate flowers** with pedicels 4.5–9 mm, glandular and very sparingly short villous; bracteoles wanting; sepals 2, elliptic to broadly transversely elliptic or suborbicular, 4.5–9 x 4.5–11 mm, entire, externally sparingly glandular and puberulous, internally white, externally white to rose pink; petals 1, oblanceolate, 4 x 1 mm; ovaries bilocular with bipartite placentae, 6.5–8 mm, sparingly glandular and puberulous, the wings marginally sparingly ciliate, green deeply suffused red; styles 3 with one often reduced in size, to 2.5 mm, fused only briefly basally; stigmas 3, 2 dilated-lunate and one sometimes reduced and lunate. **Capsules** with pedicels 10–16 mm; bodies beaked, very strongly nutant, 9.5–11 mm, very sparingly pilose, green suffused red; locule chambers externally asymmetrically elliptic, 6–6.5 mm; wings 3, unequal, the largest oblong to ovate, 9–17 x 6–11 mm, apically rounded to truncate, marginally sparingly finely ciliate, the second asymmetrically triangular to lunate, 3.5–5.5 x 7–8.5 mm, the third subequal to the second.

Etymology. This species is named in honor of the late Dr. Alexander Skutch (1904–2004) who first collected this species in 1940. During his long and prolific career, Skutch wrote extensively on Costa Rica and the birds of Costa Rica.

Distribution and habitat. *Begonia skutchii* can be found growing epilithically, epiphytically and terrestrially in primary forests and in seepage areas in remnant cloud forests between 180–900 m in southwestern Costa Rica. *Begonia skutchii* is one of five species in sect. *Weilbachia* known to occur in Costa Rica. Like other species in this Mexican and Central American section, its ovaries are bilocular with bipartite placentae and its capsules are nutant. Moreover, capsular dehiscence only occurs after a portion of the fleshy covering of the capsular body erodes. Although two or three styles may be present among the species, the third, when present, not infrequently is smaller and less developed with a smaller stigmatic surface (Burt-Utley & Utley 1999). Species in the section have both staminate flowers and pistillate with an inner perianth series like *B. skutchii*, while others simply have apetalous flowers in both sexes. This latter condition can be observed in *B. copeyana* C. DC. and *B. vestita* C. DC. from Costa Rica, as well as in other species in the section from Central America and México. An unusual character that can be observed in *B. skutchii* and only occurs in sect.

Weilbachia in Mexico and Central America is its finely pustulate upper leaf surfaces with some of the pustules terminating in stout villi. Depending upon specimen preparation, the lower leaf surface of *B. skutchii* will appear finely alveolate. *Begonia skutchii* shares with *B. turrialbae* Burt-Utley & Utley its unusual pustulate upper leaf surfaces. In contrast, *B. carletonii* has upper leaf surfaces that are finely beaded, appearing at most very shallowly papillose. When inflorescences of *B. skutchii* are compared with these latter species, those of *B. skutchii* are strongly asymmetric and several to many-flowered, while those of *B. turrialbae* are unilateral, typically producing a flower and a branch at each node and ending with a single terminal flower. In contrast, inflorescences of *B. carletonii* are symmetric and few-flowered.

Specimens examined. COSTA RICA. San José. Basin of El General, 675–900 m, Mar 1940, *Skutch 4864* (CR, US); 9.9 km SW of Río Pacuare and 3.1 km N of Tinamastes in Fila Tinamastes along rd from Dominical to San Isidro, ca. 3200 ft, 30 Jul 1983, *Utley & Utley 7238* (BM, C, CAS, CR, DUKE, F, GH, MO, NY, US, USF); 14.5 km W of square in San Isidro de El General along road to Dominical, 900 m, 21 Feb 1987, *Utley & Utley 8237* (CAS, DUKE, MEXU, MO). **Puntarenas.** Cantón de Golfito, Dos Brazos de Río Tigre, Jiménez, Cerro Müller, bajando por la fila a las afluentes de Río Niño, 8° 30' 35" N, 83° 28' 35" W, 400–744 m, 30 Aug 1990, *Herrera & Fallas 4172* (MO); Cantón de Osa, Sierpe, San Juan, Cuenca superior del Río Dan Juan, estribaciones Cerros Chocuaco, 8° 43' 50" N, 83° 33' 05" W, 580 m, 29 Jan 1991, *Herrera 4894* (USF). **Limón.** Cordillera de Talamanca along ridge between Quebrada Camagre and Río Barbilla, 10° 00' N, 83° 24.5' W, 180–480 m, 9 Sep 1988, *Grayum, Robles & Martínez 8918* (MO, USF); Cordillera de Talamanca, Cantón de Matina, Formation Caliza Río Barbilla, 10° 00' 30" N, 83° 25' W, 200–300 m, 18 Oct 1988, *Herrera 2208* (MO).

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NEW VASCULAR PLANT RECORDS FOR FAR SOUTH TEXAS

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ABSTRACT

Coccoloba uvifera (Polygonaceae), sea grape, is reported for the first time as adventive in Texas, in the Gulf Prairies and Marshes vegetational region of Cameron County. It is used as an ornamental in the more southern part of Texas Gulf Coast. *Ophioglossum engelmannii* (Ophioglossaceae), limestone adder's tongue, is reported from Boca Chica, Cameron County, also in the Gulf Prairies and Marshes region. This location is approximately 365 km south of the previously known southern station in Texas (Wilson County) and 320 km northeast of the northwesternmost known Mexican occurrence in central Nuevo Leon.

The following vascular plant records are a result of collections made between November 18 and 20, 2013, in the Gulf Prairies and Marshes region of coastal Cameron County, Texas.

Coccoloba uvifera (L.) L. (Polygonaceae), Sea-grape. Figure 1.

Voucher specimens. **TEXAS**. Cameron Co.: 0.3 mi S of Jct of Hwy 100 and Padre Blvd on Padre Blvd, W side of Padre Blvd. in undeveloped natural coastal prairie on edge of black mangrove dominated tidal flats, 20 Nov 2013, *Singhurst 20463* (BAYLU); 0.1 mi ENE of Jct of Wallace L. Reed Road and Padre Blvd in undeveloped natural coastal prairie on edge of deflational wetland and prairie transition, 20 Nov 2013, *Singhurst 20464* (BAYLU).

Sea grape is native to southern North America (including Mexico), South America, and the West Indies. Within the USA, the species is considered native to the coastal areas of central and southern Florida and coastal Mississippi (Freeman 2005; USDA, URCS 2013). Although used as an ornamental in Gulf coastal Texas, the species has not been reported as native or naturalized in the Texas (Correll & Johnston 1970; Hatch et al 1990; Turner et al 2003). Jones et al (1997) included the species in the checklist of the vascular plants of Texas but noted that it is cultivated. It is probable that the adventive plants cited below originated from ornamental specimens in the South Padre Island area. But it cannot be discounted that the Texas specimens may have originated from naturally occurring populations in adjacent Tamaulipas, Mexico, where the species was reported by Standley (1922). Regardless of origin, the species may now be reported as naturalized within the state. The small size of the plants (see Fig. 1) discloses that the introduction is fairly recent, perhaps suggesting that plants of the species are but short-lived in the state.

Associated vegetation at site *20463* included *Schizachyrium littorale, Sophora tomentosa, Iva frutescens, Spartina spartinae, Solidago sempervirens, Borrichia frutescens, Andropogon glomeratus, Palafoxia texana,* and *Avicennia germinans*. Common associates (at site *20464*) included

Figure 1. *Coccoloba uvifera (Singhurst 20463*, BAYLU). In the background is the lower Laguna Madre. Photo by Singhurst.

Schizachyrium littorale, Conoclinium betonicifolium, Paspalum monostachyum, Spartina spartinae, Solidago sempervirens, Andropogon glomeratus, Baptisia sp., and *Eleocharis* spp.

The species appears to have potential to spread northward because of more favorable conditions present in that direction (increased frost-free period and greater precipitation, see Gould 1962, p. 5) or from spread of cultivated stock. At this time, *Coccoloba* does not seem to present serious invasive potential.

Ophioglossum engelmannii Prantl (Ophioglossaceae), Limestone adder's tongue. Figure 2.

Voucher specimen. **TEXAS**. Cameron Co.: Boca Chica State Park, 0.1 mi N of jct of Eichorn Rd and Boca Chica Blvd (Hwy 4) on Eichorn Rd to entrance of state park, then 0.9 mi E on road that heads to South Bay and lies adjacent to South Bay, then 30 mi SE from bay edge, ca. 4 m elevation, 18 Nov 2013, *Singhurst 20462* (BAYLU).

The species was found at the base of a loma shrub thicket beneath clumps of *Aristida purpurea* var. *nealleyi*, *Spartina spartinae*, *Schizachyrium littorale*, *Bothriochloa laguroides*, *Cenchrus spinifex*, *Oxalis dichondrifolia*, and *Rhynchosia americana*. This fern occurred at 4 m above mean sea level on Point Isabel clay loam soils, which are deep, well drained, and calcareous.

This record was unexpected, particularly in view of Wherry's (1927) description of this region of Cameron County as "a fernless area." In fairness to Wherry, his statement appeared mainly

directed toward the Polypodiaceae (sensu lato of that time) and not the fern allies (i.e., Equisetaceae) or what he considered non-typical ferns (e.g., Marsileaceae, Azollaceae). Nonetheless, the only fern he observed was *Marsilea vestita*. This view appears supported by Turner et al. (2003), who map only three species of ferns or fern allies in Cameron County, one species each for the three mentioned families.

Ophioglossum engelmannii is readily distinguishable by its fleshy, dull green sterile fronds with apiculate points (Palmer 1919) and principal veins of sterile frond forming primary areoles in which are included numerous veinlets forming secondary areoles (Correll & Johnston 1970). The plants are said to normally occur in thin, often clayey, soil over limestone (Clausen 1938). The small number of taxonomic characters, described as "trivial details" by Clausen 1938, seems partly responsible for the difficulty of circumscription of species in the genus and apparently may complicate specific recognition. Thieret (1980) reported that *O. engelmannii* has a very distinctive odor by which it can be identified even after 5 years of storage. The odor is described in the key to species as malodorous.

Figure 2. *Ophioglossum engelmannii* (*Singhurst 20462*, BAYLU). Photo by Singhurst.

The Cameron County record is notable for extending the known distribution of the species southward in the state and in substantially revising the minimum elevation that the species is known to occur. It is the southernmost record of the species in the state, being approximately 365 km south of the nearest known Texas location, Suterland [Sutherland] Springs, Wilson County (*H.B. Parks s.n.*, TEX), which is located at the southern limits of the Post Oak Savannahs. It also appears to be the only record of *Ophioglossum engelmannii* in the Gulf Marshes and Prairies vegetational region south

of Harris County (specimens cited in Correll 1956, where locations are given to county only), about 470 km to the north. The species is mapped as present in the South Texas Plains and the southern portion of the Gulf Prairies and Marshes vegetation regions by Wagner and Wagner (1993) but not in Turner et al. (2003). South of Texas, the species is [presumably] in limestone regions at elevations from 1000-2650 m (Mickel and Smith 2004). The Mexican record nearest to the Cameron County record is this: **Nuevo Leon**. Mpio. Galeana: Rancho Aguililla, 1850 m, *Hinton et al. 25489* (MO, Tropicos 2013), which is about 320 km southwest of Boca Chica, Texas. Concerning elevation, *Singhurst 20462* occurred at 4 m, which is below the range of elevations (50-1000) reported in Wagner and Wagner (1993) and the 1000-2650 m elevations of Mickel and Smith (2004). More specific information about the distribution of the species may be found in the references cited.

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A NEW SERIES AND A VALIDATED VARIETAL NAME IN *CRATAEGUS* (ROSACEAE)

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ABSTRACT

Transfer of *Crataegus silvicola* Beadle to ser. *Tenuifoliae* requires providing a new name for the remainder of ser. *Silvicolae*, as *C. silvicola* was the type element of that series. The new series is **Crataegus** ser. **Populneae** J.B. Phipps, **ser. nov**. The paper also validates **C. schuettei** var. **cuneata** Kruschke ex J.B. Phipps, **var. nov.**

Recognition of *Crataegus* ser. *Populneae*

Crataegus silvicola Beadle (Bot. Gaz. 28(6): 414–416, 1899) is to be transferred from ser. *Silvicolae* to ser. *Tenuifoliae* in the author's treatment of *Crataegus* for vol. 9 (Rosaceae) of the forthcoming Flora of North America. It will be treated there as *C. iracunda* Beadle, which is considered synonymous. *Crataegus silvicola* Beadle is an illegitimate later homonym of *C. silvicola* Gandoger (Bull. Soc. Bot. France 18: 448. 1872). This transfer thus deprives the remainder of the ser. *Silvicolae* of any name. I select *Crataegus populnea* Ashe as the type of the new series and name the new series after it.

CRATAEGUS ser. **POPULNEAE**, J.B. Phipps, **ser. nov**. **TYPE**: *Crataegus populnea* Ashe

Shrubs or trees, (1–)2–7(–8) m, main trunk dominant. **Stems:** trunk bark buff to gray-brown, plated and somewhat exfoliating, freshly exposed orange-brown; twigs +/- straight, at 1-year old reddish brown or dark reddish brown, sometimes tan, at 2-years old +/- gray, sometimes gray-brown or blackish, older paler gray; thorns on twigs moderately frequent, straight to recurved, 1-year old usually dark reddish brown to blackish, usually shiny, usually slender, 2.5–5 cm. **Leaves**: petioles (16–)30–55% length of blade, usually glabrous, eglandular or sparsely glandular, if so, usually sessile-glandular; blades mid to dark green adaxially, broadly elliptic to ovate or deltate, rarely suborbiculate or rhombic, 2–7(–8) cm, chartaceous to subcoriaceous, base broadly cuneate or rounded to truncate or subcordate, lobes 3–5 per side, sinuses shallow to deeper, margins serrate, teeth numerous; veins 3–5(–6) per side, apex +/- acute, abaxial surface glabrous except sometimes for veins, adaxial pubescent young. **Inflorescences** 4–10(–12)-flowered, convex panicles; branches usually glabrous, sometimes pubescent; bracteoles absent or few, caducous, linear, membranous, margins sessile-glandular. **Flowers** 14–18 mm diam.; hypanthium usually glabrous; sepals triangular or lanceolate, much shorter than petals, margins subentire or shallowly to moderately glandular-serrate; stamens 6—10 (20), anthers usually pink or rose to purple, rarely yellow; styles 3–5. **Pomes** usually bright red, suborbicular to oblong or pyriform, 8–12(–13) mm diam., usually somewhat pruinose, glabrous; flesh usually hard, sometimes mellow; sepals erose or persistent, non-accrescent; pyrenes 3–5, sides smooth.

Species 8: eastern USA and adjacent Canada.

Crataegus ser. *Populneae* constitutes an assemblage of mainly rare or sporadically distributed species, most of them held to be in some manner intermediate between ser. *Tenuifoliae* and ser. *Pruinosae*. An exception to this generalization is the local southeastern USA *Crataegus aemula*

Beadle, which has stipitate-glandular petioles and is quite hairy, now only retained in ser. *Populneae* out of convenience. *Crataegus populnea*, selected as the type of the new series, is not only by far the most abundant species but also well exemplifies the intermediacy mentioned above. Also, there is a beautiful type specimen of it at PH.

Validation of *Crataegus schuettei* var. *cuneata*

Crataegus schuettei Ashe var. *cuneata* was provided with a detailed and well-illustrated protologue (Milwaukee Public Mus. Publ. Bot. 3: 80-81, 1965). However, Kruschke's normal practice was to provide two 'co-types' both from the same labeled tree, even though this was explicitly against the code of the time, so the names of most of his new taxa were not validly published. One of Kruschke's varietal names is validated here.

Crataegus schuettei Ashe var. **cuneata** Kruschke ex J.B. Phipps, **var. nov.** **TYPE: USA. Wisconsin.** Sheboygan Co.: Lyndon Twp., 12 May 1952, *E.P. Kruschke K-49-2* (holotype: MILW).

Crataegus schuettei var. *cuneata*, a variant local to two Wisconsin counties, is distinguished by its rather narrow (for *C. schuettei*) leaves with strikingly cuneate bases (particularly noticeable in flower) and pubescent inflorescences (unique in the species).

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ON THE VALIDITY OF *TRILLIUM* L. SUBG. *PHYLLANTHERUM* RAF. (MELANTHIACEAE; PARIDEAE).

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ABSTRACT

Trillium subg. *Phyllantherum*, long attributed to Rafinesque, is shown not to have been validly published in 1820. Likewise the genus name *Phyllantherum*, long thought not to exist, is shown to have been published by Nieuwland in 1913, albeit as a superfluous name. As a result, the subgeneric name was not validly proposed until inadvertently done so by J.D. Freeman in 1975.

While reviewing various names proposed by Constantin Samuel Rafinesque (1783–1840), we discovered that the commonly used name, "*Trillium* subg. *Phyllantherum*," proposed by Rafinesque in 1820 was not validly published, for while he included three species, viz., *T. sessile* L., *T. petiolatum* Pursh, and *T. tinctorum* Raf., he only provided a Latin description for *T. sessile*, which, as Rafinesque stated, belonged to a "un sous-genre, sous le nom de *phyllantherium*." He did not provide a description for his "subg. *Phyllantherum*."

The above invalidly published subgenus name is now seen in a wide variety of literature from taxonomic (Freeman 1975: 3; Case 2002: 106), ecological (Bock et al. 1989: 96), horticultural (MacGary 1996: 365; Matthews 2011: 160), rare plant investigations (Chafin 2007: 496), and molecular studies (Osaloo et al. 1999; Farmer & Schilling 2002; Schilling et al. 2013).

Rafinesque's subgenus name was first validated as an unranked infrageneric name, *Trillium* L. [unranked] *Phyllantherum*, by Schultes and Schultes f. (1830: 1497); these authors referred to Rafinesque's 1820 publication. Unfortunately, the preceding valid name remained unknown to many botanists. Later the sessile-flowered trilliums were distinguished by Salisbury (1866: 61) at a higher rank when he proposed the genus *Esdra* for a single species, *T. sessile*.

At the generic level, the existence of "*Phyllantherum* Raf." was implied by several early authors (Endlicher 1836: 153; Kunth 1844: 37, 1850: 121; Spach 1846: 210; Orbigny 1848: 652; Pfeiffer 1871: 92, 1874: 692; Jackson 1893: 1119) who listed the name as a synonym. It was Nieuwland (1913: 122) who inadvertently validated the genus name. His reference to Rafinesque's 1820 publication serves as an indirect reference to Schultes and Schultes f., who also referred to Rafinesque (see Melbourne Code Art. 41.3 pertaining to new combinations made before 1953; McNeill & al. 2012). At the same time, Nieuwland established *P. recurvatum* (Beck) Nieuwl. and *P. sessile* (L.) Nieuwl.

Although *Phyllantherum* Nieuwl. was validly and legitimately established, it was superfluous when published. This is because of Nieuwland's citation of *Esdra* as a generic synonym.

When Freeman (1975: 1–3) revised the sessile-flowered trilliums, he assigned them to the subg. *Phyllantherum* (p. 2), which he attributed to Rafinesque without comment. In doing so, Freeman inadvertently validated his subgenus by a full and direct reference to *Phyllantherum* Nieuwl. (p. 3). As in the case of Nieuwland (l.c.), Freeman also did not refer to Schultes and Schultes f. (l.c.), but cited *Esdra* as a synonym. For post-1952 new combinations lacking a direct reference to the basionym, one may apply Art. 41.8a and Ex. 19 and treat Freeman's inadvertent new combination as validly made based on the 1830 Schultes and Schultes f. name.

In summary:

Trillium L. subg. *Phyllantherum* Raf., J. Phys. Chim. Hist. Nat. Arts 91: 72. 1820, nom. inval. (as "*Trillium*").

Trillium L. [unranked] *Phyllantherum* Schult. & Schult. f. in J.J. Roemer., Syst. Veg. 7(2): 1497. Oct-Dec 1830. – **TYPE**: not designated; **LECTOTYPE**: *T. sessile* L. (vide J.D. Freeman (1975: 2).

Esdra Salisb., Gen. 60. Apr-Mai 1866. – **TYPE**: *Trillium sessile* L..

Phyllantherum (Schult. & Schult. f.) Nieuwl., Amer. Midl. Naturalist 3: 112. Jul 1913 (nom. superfl. for *Esdra*)

Trillium L. subg. *Phyllantherum* (Schult. & Schult. f.) J.D. Freeman, Brittonia 27: 2. 30 Mar 1975.

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THE NATIONAL WETLAND PLANT LIST: 2014 UPDATE OF WETLAND RATINGS

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ABSTRACT

The U.S. Army Corps of Engineers (Corps) administers the National Wetland Plant List (NWPL) for the United States (U.S.) and its territories. Responsibility for the NWPL was transferred to the Corps from the U.S. Fish and Wildlife Service (FWS) in 2006. The list was updated in 2012, and the Corps led an interagency effort to revise the list again in 2013. As part of the authorization of the revised NWPL in 2012, new methods were adopted for annual updates to the scientific names, regional distribution, and wetland ratings. This paper presents the third update of the list under Corps administration. The 2012 list contained 7,828 species, and the 2013 update contained 7,937 species. As part of the BONAP (Biota North America Program) database used for the 2013 update, there were 754 reports of species of wetland plants with new range extensions within the 10 Corps wetland regions. Also, BONAP and other users requested that 124 other species be added to the NWPL, which increases the number of species to 8061. These 878 species were evaluated and rated by Regional Panels and by the National Panel representatives from four agencies. The inclusion of these species represent the 2014 update to the NWPL.

BACKGROUND

Since the Corps assumed administrative responsibilities for the NWPL in 2006, the list has gone through an extensive updating process that culminated in its authorization for national use in May 2012 (Federal Register 2012; Lichvar 2012). The development of the 2012 list was a cooperative effort between four federal government agencies: the Corps, the FWS, the U.S. Environmental Protection Agency (EPA), and the Natural Resources Conservation Service (NRCS). The effort was managed by a National Panel consisting of representatives from the four agencies. The 2012 NWPL is the standard reference for wetland indicator status ratings of vascular plants in the United States and territories, and is used for many purposes, including wetland delineation, assessment, mitigation, and habitat restoration. The NWPL is available to all users through a web application (http //wetland_plants usace army mil/).

The 2012 update built on the legacy of the FWS's 1988 (Reed 1988), 1993 Region 9 (Northwest) Supplement (Reed, 1993), and draft 1996 wetland plant lists. It updated all taxonomic views and nomenclature in accordance with BONAP and revised wetland ratings (Lichvar and Minkin 2008). Additionally, the 2012 revision included several changes to the management of the NWPL, along with revised definitions of wetland categories, new Corps geographic wetland regions, protocols for challenging wetland ratings, and procedures for annual revisions.

As with previous versions of the wetland plant list, the 2012 NWPL and updates support wetland delineation efforts under Sec. 404 of the Clean Water Act and the Swampbuster provisions of the Farm Bill (as amended), and it is used in the National Wetland Inventory Program. To accomplish this more effectively, the Corps re-aligned the NWPL's geographic regions to correspond to those of federal wetland efforts, including the interagency wetland delineation manual and its regional wetland delineation supplements. The NWPL is now divided using the 10 regional Corps wetland delineation regions for the U.S. and its territories (Wakeley 2002) (Fig. 1). Included within four of these Corps regions are 17 subregions in which small numbers of wetland plants have wetland ratings that differ from the ratings for the same plants in the rest of the region.

Figure 1. Geographic regions for the 2012 NWPL, based on Corps regions.

The five wetland rating categories in the NWPL were developed in the 1980s by Reed (1988). Each plant species was assigned a rating representing the estimated probability, or frequency, with which it was thought to occur in wetlands, as opposed to non-wetlands, across its entire range. The 1988 ratings were divided into categories based on quantitative ranges of frequency, but the 2012 ratings were based on simpler qualitative definitions (Lichvar et al. 2012) (Table 1). Indicator status ratings are now assigned to each species based on a review of the botanical literature and herbarium records, along with the best professional judgment of national and regional experts. Longer quantitative rating definitions are still used, but only for field testing of wetland ratings.

Table 1. Short qualitative descriptions of the five wetland indicator status ratings used to determine if vegetation is hydrophytic during wetland delineations in the United States

Indicator status	Designation	Qualitative Description
Obligate (OBL)	Hydrophyte	Almost always occur in wetlands
Facultative Wetland	Hydrophyte	Usually occur in wetlands, but may occur in non-
Facultative (FAC)	Hydrophyte	Occur in wetlands and non-wetlands
Facultative Upland	Nonhydrophyte	Usually occur in non-wetlands, but may occur in
Upland (UPL)	Nonhydrophyte	Almost never occur in wetlands

ANNUAL UPDATE PROCESS

As part of the 2012 NWPL update, representatives from each of the four Federal agencies responsible for the NWPL agreed on new protocols and procedures for managing the list. These procedures were described in the 2012 Federal Register announcement for updating the NWPL. Under the NWPL authorization, it is now possible to update and maintain the list annually so that the nomenclature and taxonomy do not become outdated and wetland ratings can be refined as new information becomes available. In particular, the annual NWPL updates will include additions or deletions to the list; modifications to wetland indicator statuses that were revised during the previous year; and updates of the nomenclature, taxonomy, and geographic distribution of species on the NWPL.

The annual update of the list has two steps. First, this and previous updates to the database for nomenclature, taxonomy, and U.S. state/Canadian province and U.S. county-level phytogeography have been made by Dr. John Kartesz of BONAP. Second, input from the public, as well as from federal and state agencies, is used to modify wetland ratings by processes of evaluation that are similar to those used during the 2012 update. These requests may include adding new species to the list.

The annual update is released in three parts: 1) the NWPL web site is updated to reflect any modifications from the previous year, 2) a series of downloadable files for the Corps regions and states is made available via the web site, providing local lists of wetland species and their wetland indicator ratings, and 3) the national list is published and subdivided by Corps regions. This publication represents the third component of the 2014 update.

THE 2014 NWPL UPDATE

The 2012 NWPL contained 7,828, and the 2013 NWPL contained 7,937 wetland plants for the United States and its territories. The 2014 NWPL has increased to 8,061 wetland plants, mainly because of newly suggested additions to the list and geographic range extension reports for species new to a Corps wetland region. The 2014 NWPL update is in the Appendix A.

The 2014 NWPL update list is based on the database we received from BONAP in 2013 and used in generating the 2013 NWPL update. Included in the 2013 BONAP database were 754 species with new geographic range extensions in Corps wetland regions and 123 species proposed for consideration to be added to the NWPL. We postponed evaluating these species until 2014. In addition, the National Panel (NP) requested that *Lonicera japonica* Thunb. occurring in the Atlantic and Gulf Coastal Plain be reevaluated by that Regional Panel (RP).

For the 2014 NWPL update, we evaluated and rated 878 species. The first step in the updating process was to see if any of these species occurred in other Corps regions. If they did and if they were rated in two or more regions with the same wetland rating, we assigned the same wetland rating to the species in the new geographic region. This group then was referred to as the "auto assigned" group. If a species had only one other rating or the ratings varied across the Corps regions, we moved it to the next step. There were 294 species in the auto assigned group. The remaining species were evaluated by a Regional Panel (RP) consisting of one representative from each of the four agencies within the Corps regions where the species occurs. The RP reviewed the literature, interviewed other professional botanists, and used their personal field observations to assign wetland ratings. The RPs, by consensus, assigned ratings to 450 species. Those species for which the RP did not reach consensus were then evaluated and rated by the NP. The NP assigned wetland ratings for 246 species. The culmination of these steps and assigned rating then represent the 2014 efforts to update the NWPL.

ACKNOWLEDGEMENTS

Many people, agencies and organizations are involved in maintaining and improving the accuracy of the NWPL, and they are all thanked for their support and input. The bulk of the effort and thanks goes to the National and Regional Panel members across the country who dedicate significant time and energy responding to requests to evaluate endless lists of wetland plants. Many people in the public sector have made valuable suggestions and input about wetland species. Underlying these efforts is the work of several key people, who are thanked: John Kartesz at BONAP, who keeps the database updated, and Misako Nishino, who maintains the BONAP database; Rick Bates, who manage to keep millions of data points in the right places; and Jennifer Gillrich and Lindsey Lefebvre, who make it all happen. We thank the Wetland Regulatory Assistance Program of the U.S. Army Corps of Engineers for funding these efforts.

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Appendix A. Species evaluated for inclusion in the 2014 NWPL. In the ratings, 2 indicates the auto-assigned group, 3 indicates species evaluated by a Regional Panel, and 4 indicates species evaluated by the National Panel.

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Abies procera			3-FACU										Noble Fir
Acalypha poiretii					3-FACU				3-FACU				Poiret's Copperleaf
Acer glabrum								3-FAC					Rocky Mountain Maple
Achillea ptarmica		3-FACU	4-FACU		3-FACU	3-FACU		3-FACU		3-FACU	4-FACU		Pearl Yarrow
Achyranthes aspera					3-UPL								Devil's-Horsewhip
Aconitum uncinatum		3-FAC						3-FAC	3-FAC				Southern Blue Monkshood
Actaea podocarpa								4-FAC					Mountain Bugbane
Aegilops tauschii									3-UPL				Tausch's Goat Grass
Aeschynomene americana					2-FAC								Shyleaf
Agalinis calycina										2-OBL			Leoncita False Foxglove
Agalinis flexicaulis	New	3-FACW											Hampton False Foxglove
Agalinis skinneriana		4-FACU			3-FACU	3-FACU		4-FACU					Skinner's False Foxglove
Ageratina altissima										3-FACU			White Snakeroot
Ageratum conyzoides			4-FACU		3-FACU								Tropical Whiteweed
Ageratum houstonianum			2-FACU		2-FACU	2-FACU							Bluemink
Agoseris X montana			2-UPL										[*aurantiaca X glauca*]
Agnmonia parviflora			4-FAC							3-FACW			Harvestlice
Agrostis castellana		2-UPL			2-UPL								Dryland Bent
Agrostis lacuna-vernalis	New		4-FACW										unknown
Aletris farinosa			2-FAC			2-FAC							White Colicroot
Alhagi maurorum		2-FAC			2-FAC								Camelthorn
Alisma plantago-aquatica									2-OBL				European Water-Plantain
Allium bisceptrum						3-FACU							Aspen Onion

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Alnus glutinosa						2-FACW							European Alder
Alocasia macrorrhizos			3-FACW			3-FACW							Giant Taro
Alternanthera ficoidea		2-FACU				2-FACU							Sanguinaria
Amaranthus acanthochiton		2-FACU											Greenstripe
Amaranthus californicus								2-FACW					California Amaranth
Amaranthus crassipes									3-FAC				Spreading Amaranth
Amaranthus obcordatus										2-FACU			Trans-Pecos Amaranth
Amaranthus spinosus										2-FACU			Spiny Amaranth
Ambrosia artemisiifolia											4-FACU		Annual Ragweed
Ambrosia trifida											2-FAC		Great Ragweed
Amelanchier arborea			4-FACU										Downy Service-Berry
Amorpha confusa	New	4-FACU											Carolina Indigo-Bush
Ampelaster carolinianus					3-FACW								Climbing Aster
Ampelopsis arborea			4-FACU							3-FAC			Peppervine
Ampelopsis cordata			2-FAC										Heart-Leaf Peppervine
Amphicarpaea bracteata			3-FACW										American Hog-Peanut
Amphitecna latifolia				4-FAC									Black-Calabash
Anaphalis margaritacea		4-UPL	3-FACU		3-UPL	3-FACU		3-FACU	3-FACU		3-UPL		Pearly-Everlasting
Andropogon bicornis							2-FAC						Barbas-de-Indio
Andropogon glaucopsis					3-FACW								Coastal Bluestem
Andropogon hirsutior	New	3-FACW			4-FACW	4-FACW			3-FACW				unknown
Angelica inquinata		2-UPL											Filmy Angelica

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Anthenantia rufa						4-FACU							Purple Silkyscale
Anthoxanthum hirtum		3-FACW	3-FACW			3-FACW		3-FACW	3-FACW	3-FACW	3-FACW		Northern Sweet Vernal Grass
Antigonon leptopus					4-FACU								Queen's-Jewels
Aplectrum hyemale			2-FAC							2-FAC			Adam-and-Eve
Arabis alpina										2-FAC			Alpine Eared Rockcress
Arabis eschscholtziana						2-FACU			2-FACU				Pacific-Coast Eared Rockcress
Aristida beyrichiana					4-UPL								Beyrich's Three-Awn
Aristida spiciformis						4-FAC							Bottlebrush Three-Awn
Arivela viscosa									3-FACU				Tickweed
Aronia melanocarpa										3-FACW			Black Chokeberry
Artemisia campestris	New	3-UPL	4-UPL		3-UPL	3-UPL		4-UPL	4-UPL	3-FACU	3-UPL		Pacific Wormwood
Artemisia tilesii						2-FACU							Tilesius' Wormwood
Asclepias speciosa		2-FAC											Showy Milkweed
Asclepias subverticillata		4-FACU											Horsetail Milkweed
Asclepias viridula					3-FACW								Southern Milkweed
Astragalus diphysus	New	3-UPL	3-UPL			4-UPL				3-FACU			Speckle-Pod Milk-Vetch
Athyrium angustum			2-FAC										Northern Lady Fern
Atriplex alaskensis										4-FACU			Alaska Orache
Atriplex glabriuscula						2-FACU							Scotland Orache
Atriplex hortensis		3-FAC											Garden Orache
Atriplex mucronata			4-FACU										Crested Saltbush
Atriplex stipitata	New		3-UPL										Mallee Saltbush
Axonopus compressus										3-FAC			Broad-Leaf Carpet Grass
Azolla cristata									2-OBL				Crested Mosquito Fern
Azolla pinnata					3-OBL								Asian Mosquito Fern
Bacchanis glomeruliflora					4-FAC								Silverling

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Baccharis neglecta					2-FAC			2-FAC					Roosevelt-Weed
Bacopa innominata					2-OBL								Tropical Water-Hyssop
Bambusa bambos	New	3-FACU			3-FACU								Giant Thorny Bamboo
Bambusa vulgaris					3-FACU								Feathery Bamboo
Baptisia australis		3-FACU				4-UPL		3-FACU	3-FACU				Blue Wild Indigo
Barbarea vulgaris											3-FACU		Garden Yellow-Rocket
Barkleyanthus salicifolius		2-FAC				2-FAC							Barkley's-Ragwort
Bassia hirsuta								2-OBL					Hairy Smotherweed
Betula murrayana								3-FACW					Murray's Birch
Betula pendula		2-FACU	2-FACU		2-FACU	2-FACU		2-FACU					European Weeping Birch
Betula X sandbergii			2-OBL							2-OBL			[*papyrifera X pumila*]
Bidens aristosa										2-FACW			Bearded Beggarticks
Bidens eatonii		3-FACW			4-FACW								Eaton's Beggarticks
Bidens laevis								2-OBL					Smooth Beggarticks
Bidens mitis								2-OBL					Small-Fruit Beggarticks
Bidens tenuisecta		3-FACW			3-FACW								Slim-Lobe Beggarticks
Boechera collinsii											3-UPL		unknown
Borrichia frutescens					3-OBL								Bushy Seaside-Tansy
Bothriochloa barbinodis								4-UPL					Cane Beard Grass
Botrychium lunaria		3-FAC			4-FAC								Common Moonwort
Botrychium pinnatum						4-UPL							Northeastern Moonwort
Brachyelytrum erectum		4-FACU		4-FACU		4-FACU		3-FACU	3-FACU				Bearded Shorthusk
Braya glabella						4-FACU							Smooth Northern-Rockcress
Braya humilis						4-FACU							Alpine Northern-Rockcress
Bromus madritensis					3-UPL								Compact Brome

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Brugmansia versicolor	New	4-UPL			3-FACU								Arborescent Angel's-Tears
Bulbostylis funckii						2-FACW							Funck's Hair Sedge
Bulbostylis juncoides										2-FACW			Rush Hair Sedge
Bulbostylis stenophylla					3-FACU								Sandy-Field Hair Sedge
Caladium bicolor							4-FAC						Heart-of-Jesus
Calandrinia ciliata		2-FACU											Fringed Redmaids
Callisia repens							2-FACU						Creeping-Inchplant
Callitriche stagnalis						2-OBL							Pond Water-Starwort
Callitriche stenoptera	New		3-OBL			3-OBL		3-OBL		3-FACW	3-OBL		Narrow-Wing Water-Starwort
Calluna vulgaris					2-FAC								Heather
Calydorea coelestina					3-FACW								Enchanting Violet-Lily
Camelina alyssum								2-FACU					Madwort False Flax
Campanula aparinoides			2-OBL										Marsh Bellflower
Canna flaccida			3-OBL		3-OBL	3-OBL							Bandanna-of-the-Everglades
Canna glauca					2-OBL								Brazilian Arrow-Wood
Canna indica					4-FACW								Indian-Shot
Cardamine clematitis		3-FAC											Small Mountain Bittercress
Cardamine douglassii						4-FACW							Limestone Bittercress
Cardamine flexuosa						3-FACW							Woodland Bittercress
Cardamine impatiens		3-FAC						3-FAC	3-FAC				Narrow-Leaf Bittercress
Cardamine nymanii	New										3-FACW		unknown
Cardamine X incisa					3-FACU								(*concatenata* X *maxima*)
Cardiospermum halicacabum			3-FAC										Love-in-a-Puff
Carex arkansana									3-FAC				Arkansas Sedge
Carex austrina									2-FACU				Southern Sedge
Carex austrodeflexa	New	3-FACW			4-OBL								Canebrake Sedge

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Carex baileyi								4-FACW					Bailey's Sedge
Carex bebbii		2-OBL											Bebb's Sedge
Carex bulbostylis					2-FACW								False Hair Sedge
Carex cherokeensis									2-FACW				Cherokee Sedge
Carex corrugata									2-FACW				Prune-Fruit Sedge
Carex divulsa			2-FAC					2-FAC		2-FAC			Grassland Sedge
Carex egglestonii			3-FACU			4-FACU							Eggleston's Sedge
Carex exsiccata						2-OBL							Western Inflated Sedge
Carex extensa					2-OBL								Long-Bract Sedge
Carex fissuricola						3-FACW							Cleft Sedge
Carex foenea		4-FACU											Bronze-Head Oval Sedge
Carex frankii												2-OBL	Frank's Sedge
Carex gynocrates		2-OBL			2-OBL								Northern Bog Sedge
Carex laxiflora						4-FACU							Broad Loose-Flower Sedge
Carex lonchocarpa								2-OBL	2-OBL				Southern Long Sedge
Carex luzulifolia						2-FACW							Little-Leaf Sedge
Carex luzulina						2-OBL							Woodrush Sedge
Carex macrocephala		4-FAC											Big-Head Sedge
Carex mitchelliana								4-FACW					Mitchell's Sedge
Carex nigromarginata						4-FAC							Black-Edge Sedge
Carex oklahomensis									3-OBL				Oklahoma Sedge
Carex parryana									3-FACW				Parry's Sedge
Carex radiata		2-FAC				2-FAC		2-FAC					Eastern Star Sedge
Carex reniformis								3-FACW					Kidney-Shape Sedge

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Carex retroflexa		4-FACU				3-FACU		3-FACU	3-FACU				Reflexed Sedge
Carex rosea		3-FACU	3-FAC			3-FACU		4-FACU	4-FACU	3-FACU			Rosy Sedge
Carex salina	New								4-FACW				Saltmarsh Sedge
Carex schweinitzii		2-OBL											Schweinitz's Sedge
Carex senta						2-OBL							Western Rough Sedge
Carex squarrosa						3-FACW							Squarrose Sedge
Carex suberecta			2-OBL			2-OBL							Prairie Straw Sedge
Carex sylvatica					2-FACU								European Woodland Sedge
Carex torta						3-FACW							Twisted Sedge
Carex triangularis									3-OBL				Eastern Fox Sedge
Carex X aestivaliformis								2-FAC					[*aestivalis X gracillima*]
Cartrema americana			2-FAC			2-FAC							Devilwood
Cayaponia quinqueloba						2-FAC		2-FAC					Five-Lobe-Cucumber
Celastrus orbiculatus						4-UPL							Asian Bittersweet
Celtis laevigata										3-FACW			Sugar-Berry
Cenchrus americanus									3-FACU				Pearl-Millet
Cenchrus ciliaris									3-UPL				Buffel Grass
Cenchrus polystachios						4-FACU							Mission Grass
Centaurea cyanus											4-UPL		Garden Cornflower
Centaurea jacea		4-FACU	3-FACU		3-FACU	3-FACU		3-FACU		3-FACU			Brown-Ray Knapweed
Centaurea X moncktonii	New	3-FAC	3-FACU		3-FAC	3-FACU		3-FACU	3-FACU	3-FAC			[*jacea x nigra*]
Centella asiatica										3-FAC			Asiatic Spadeleaf
Centipeda minima		3-FAC	3-FAC		4-FACU								Spreading-Sneezeweed
Centromadia pungens									3-FAC				Pungent False Tarplant
Ceratophyllum muricatum									2-OBL				Prickly Hornwort
Cestrum nocturnum					3-UPL								Night Flowering-Jassamine

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Chamaecrista fasciculata										2-FACU			Sleepingplant
Chasmanthium latifolium										3-FAC			Indian Wood-Oats
Chasmanthium nitidum					3-FACW								Shiny Wood-Oats
Chelone obliqua						2-OBL							Red Turtlehead
Chenopodium fremontii					3-FACU				3-FACU				Fremont's Goosefoot
Chenopodium macrospermum					2-FACW								Large-Seed Goosefoot
Chrysosplenium rosendahlii	New										3-FACW		Rosendahl's Golden-Saxifrage
Cinnamomum camphora										3-UPL			Camphortree
Cirsium flodmanii		3-FAC			4-FAC								Flodman's Thistle
Cirsium horridulum								4-FACU					Yellow Thistle
Cirsium lecontei					3-FACW								Le Conte's Thistle
Cirsium nuttallii			2-FAC			2-FAC							Nuttall's Thistle
Cirsium palustre								3-FACW					Marsh Thistle
Cirsium wrightii						3-OBL				3-OBL			Wright's Thistle
Claytonia multiscapa											2-FAC		Many-Stem Springbeauty
Claytonia parviflora											2-FACU		Streambank Springbeauty
Claytonia perfoliata		4-FACU			4-FACU								Miner's-Lettuce
Clematis crispa			3-FACW										Swamp Leather-Flower
Clematis virginiana		4-UPL	3-FAC		4-UPL				3-FACU				Evergreen Traveler's-Joy
Cleomella angustifolia					2-FAC					2-FAC			Northern Stinkweed
Clinopodium douglasii			3-FACU								3-FACU		Oregon-Tea
Clitoria ternatea					3-FACU								Asian Pigeonwings
Coleataenia longifolia	New	4-FACU			3-FACU			4-FACU	3-FACW				Long-Leaf Cut-Throat Grass
Coleataenia stipitata	New	3-FACW			4-FACW	4-FACW		3-FACW	3-FACW				Stipitate Cut-Throat Grass
Commelina benghalensis					3-FACU								Jio
Convolvulus equitans								2-FACU					Texas Bindweed

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Coreopsis integrifolia					4-FACU								Fringe-Leaf Tickseed
Corispermum welshii	New	3-UPL	3-FACU			4-UPL		3-FACU	3-FACU	3-FACU			Welsh's Bugseed
Cortaderia selloana							3-FACU						Selloa Pampus Grass
Corylus avellana			3-FACU						3-FACU				Common Filbert
Cosmos sulphureus	New	4-UPL	3-FACU	4-UPL	3-FACU	4-UPL		4-UPL	3-FACU				Sulphur Cosmos
Cotula australis					3-FAC				3-FAC				Australian Water-Buttons
Crassocephalum crepidioides			3-FACU										Red-Flower Ragleaf
Crataegus berberifolia					3-FAC	4-FAC		3-FAC	3-FAC				Barberry Hawthorn
Crataegus forbesae	New								3-FACU				Forbes' Hawthorn
Crataegus phaenopyrum						2-FAC							Washington Hawthorn
Crinum americanum					4-FAC								Seven-Sisters
Crotalaria capensis	New		3-FACU										Cape Rattlebox
Ctenium aromaticum									2-FACW				Toothache Grass
Cuphea hyssopifolia		3-FAC											False Heather
Cynanchum laeve			2-FAC										Honeyvine
Cyperus aggregatus						3-FAC							Inflated-Scale Flat Sedge
Cyperus difformis									2-OBL				Variable Flat Sedge
Cyperus distans					2-OBL								Mexican Flat Sedge
Cyperus elegans										2-FACW			Royal Flat Sedge
Cyperus eragrostis					3-FACW				3-FACW				Tall Flat Sedge
Cyperus involucratus					3-FACW			4-FACW					Alternate-Leaf Flat Sedge

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Cyperus meyenianus												4-FACW	Meyen's Flat Sedge
Cyperus parishii						2-FACW							Parish's Flat Sedge
Cyperus prolifer					3-FACW								Miniature Flat Sedge
Cyperus serotinus									2-OBL				Tidal-Marsh Flat Sedge
Cyperus sunnamensis								2-FACW					Tropical Flat Sedge
Cyperus tetragonus					3-FAC	4-FAC							Four-Angle Flat Sedge
Dalea albida	New	4-UPL			4-UPL								unknown
Dalea gracilis	New	4-FAC											Needle Prairie-Clover
Daphne mezereum										3-FACU	3-FACU		Paradise-Plant
Delphinium glaucescens						2-FACU							Electric Peak Larkspur
Dentella repens	New	3-FACW			3-FACW								Lickstoop
Deschampsia flexuosa		4-UPL				4-UPL		3-FACU	3-FACU	3-FACU	4-UPL		Wavy Hair Grass
Descurainia adenophora	New		3-FACU			4-FACU				3-FACU			unknown
Desmodium barbatum							4-FACU						Zarzabacoa-Peluda
Diarrhena obovata		4-FAC			3-FACU	4-FAC		3-FAC					Hairy Beakgrain
Dichanthelium leucothrix		4-FACW	3-FACW	4-FACW	3-FACW	3-FACW			3-FACW	3-FACW			Rough Rosette Grass
Dichondra carolinensis								3-FAC	4-FACW				Carolina Pony's-Foot
Dichondra micrantha					3-FAC								Asian Pony's-Foot
Digitaria bicornis								3-FACU					Asian Crab Grass
Digitaria horizontalis					3-FACU								Jamaican Crab Grass

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Digitaria violascens								3-FAC					Violet Crab Grass
Diodia virginiana			3-FACW							3-FACW			Virginia Buttonweed
Diphasiastrum alpinum			3-FAC			9-RST							Alpine Creeping-Cedar
Diplacus aurantiacus	New		3-FACU							3-FACU			Orange Bush-Monkey-Flower
Dipsacus laciniatus		3-FACU	3-FACU		3-FACU	4-UPL							Cut-Leaf Teasel
Ditrysinia fruticosa						4-FAC							Gulf Sebastian-Bush
Doellingeria sericocarpoides									2-FACW				Southern White-Top
Downingia pulchernima	New		4-FACW							3-FACW			unknown
Draba stenoloba						4-UPL							Alaska Whitlow-Grass
Dracopis amplexicaulis										3-FAC			Clasping-Coneflower
Drosera intermedia			2-OBL							2-OBL			Spoon-Leaf Sundew
Drosera X californica	New	3-OBL											[*filiformis X tracyi*]
Drosera X hybrida		2-OBL											[*filiformis X intermedia*]
Dryas ajanensis						4-UPL							Eight-Petal Mountain-Avens
Dryas integrifolia						2-FACU			2-FACU				White Mountain-Avens
Drymocallis cuneifolia	New		4-FAC										Wedge-Leaf Woodbeauty
Drymocallis micropetala						2-FAC							Little-Petal Woodbeauty
Dryopteris X correllii	New	4-FACW			4-FACW				3-FACW				[*carthusiana X goldiana*]
Dryopteris X mickelii		2-FAC						2-FAC					[*clintoniana X goldiana*]
Dysphania aristata	New								3-FACU		3-UPL		Aristata Wormseed
Echinochloa crus-pavonis					4-FACW								Gulf Cock's-Spur Grass
Echinochloa esculenta									3-FACU				Japanese Water Grass
Echinochloa holciformis	New		3-FACW										Decorative-Millet
Echinochloa walteri										3-FACW			Long Awn Cock's-Spur Grass
Eleocharis albida										2-OBL			White Spike-Rush
Eleocharis diandra					3-FACW								Wright's Spike-Rush

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Eleocharis geniculata					3-FACW								Capitate Spike-Rush
Eleocharis mamillata			2-OBL			2-OBL		2-OBL		2-OBL			Soft-Stem Spike-Rush
Eleocharis suksdorfiana						2-OBL							Suksdorf's Spike-Rush
Elionurus tripsacoides					4-FACW								Pan-American Balsamscale
Elodea callitrichoides	New		3-OBL							3-OBL			South American Waterweed
Elodea schweinitzii		2-OBL											Schweinitz's Waterweed
Elymus hystrix										3-FACU			Eastern Bottle-Brush Grass
Elymus villosus			2-FACU										Hairy Wild Rye
Elymus wiegandii		2-FAC											Wiegand's Wild Rye
Emilia sonchifolia								3-UPL					Lilac Tassel-Flower
Epilobium anagallidifolium					4-FAC								Pimpernel Willowherb
Epilobium minutum						2-FACU							Chaparral Willowherb
Epilobium parviflorum								3-FACW	3-FACW				Small-Flower Hairy Willowherb
Equisetum myriochaetum	New		3-OBL										Mexican Giant Horsetail
Equisetum X litorale						2-OBL							[*arvense* X *fluviatile*]
Equisetum X mackaii			4-FACW							3-FACW			[*hyemale* X *variegatum*]
Equisetum X nelsonii		4-FACW											[*laevigatum* X *variegatum*]
Eragrostis amabilis			3-FAC										Feather Love Grass
Eragrostis atrovirens					3-FAC								Thalia Love Grass
Eragrostis bahiensis					3-FAC				3-FAC				Bahia Love Grass
Eragrostis ciliaris			3-FACU						3-FACU	3-FACU			Gopher-Tail Love Grass
Eragrostis lugens								3-FAC					Mourning Love Grass
Eragrostis refracta									2-FACW				Meadow Love Grass
Eragrostis unioloides					3-FAC								Chinese Love Grass
Eremochloa ciliaris	New		3-FACU										Fringed Centipede Grass
Erigeron bellioides		4-FACU											Bellorita

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Eriobotrya japonica						4-UPL							Loquat
Eriocaulon aquaticum						2-OBL							Seven-Angle Pipewort
Eriocaulon benthamii	New	3-FACW											Bentham's Pipewort
Eriocaulon ravenelii					3-OBL								Ravenel's Pipewort
Enochloa punctata					2-FACW								Louisiana Cup Grass
Eryngium foetidum					3-FAC								Spiritweed
Eryngium hookeri					2-FACW								Hooker's Eryngo
Eulophia graminea		4-FACU											Grass-Leaf Wild Coco
Euonymus atropurpureus										3-FAC			Eastern Wahoo
Eupatorium leptophyllum					3-FACW								False Fennel
Eupatorium novae-angliae	New								3-FACW				New England Thoroughwort
Eupatorium X cordigerum		3-FAC											[*perfoliatum* X *rotundifolium*]
Euphorbia hirta										3-UPL			Pill-Pod Sandmat
Euphorbia hypericifolia										3-FACU			Graceful Sandmat
Euphrasia stricta	New								3-FACU				Drug Eyebright
Eurybia sibirica						4-FAC							Siberian Wood-Aster
Eustachys petraea									3-FACU				Pinewoods Finger Grass
Fallopia dumetorum			4-FACU										Corpse Black-Bindweed
Festuca aloha	New						4-UPL						Aloha Fescue
Festuca molokaiensis	New						4-UPL						Molokai Fescue
Filipendula ulmaria		4-FAC			3-FACW	4-FAC			4-FAC	3-FAC			Queen-of-the-Meadow
Fimbristylis annua									3-FACW				Annual Fimbry
Fimbristylis dichotoma								4-FACW					Forked Fimbry
Flaveria campestris		4-FAC											Alkali Yellowtops
Flaveria trinervia								3-FAC					Clustered Yellowtops
Fragaria chiloensis		3-FACU	3-FACU			3-FACU	4-FACU		3-FACU		3-FACU		Beach Strawberry

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Galium circaezans			3-FACU							3-FACU			Licorice Bedstraw
Galium mollugo		4-FACU	3-FACU					3-FACU	3-FACU	3-FACU			White Bedstraw
Galium palustre		2-OBL											Common Marsh Bedstraw
Gamochaeta pensylvanica									3-FACU				Pennsylvania Everlasting
Gaultheria ovatifolia						2-FAC							Western Teaberry
Gelsemium rankinii					4-FAC								Rankin's Trumpet-Flower
Gentianella wrightii						4-FACW				3-FAC			Wright's Dwarf-Gentian
Geranium robertianum		4-FACU	3-FACU		3-FACU			4-FACU	3-FACU		4-FACU		Lesser Herbrobert
Gibasis geniculata						3-FAC							Tahitian Bridalveil
Gleditsia aquatica									2-OBL				Water-Locust
Glinus radiatus								2-FACW					Spreading Sweetjuice
Glyceria declinata					3-FACW								Waxy Manna Grass
Glyceria fluitans		2-OBL											Water Manna Grass
Glyceria laxa		4-OBL							3-OBL				Limp Manna Grass
Glyceria septentrionalis							2-OBL						Floating Manna Grass
Grevillea robusta			3-UPL										Silk-Oak
Grindelia camporum		4-FACU			4-FACU								Great Valley Gumweed
Grindelia stricta											2-FACW		Oregon Gumweed
Gynandropsis gynandra									3-FACU				Spiderwisp
Habenaria quinqueseta			2-FACW			2-FACW							Long-Horn False Rein Orchid
Hackelochloa granularis					4-FACU			3-FACU					Pit-Scale Grass
Hedera helix		3-FACU	3-FACU		3-FACU	4-UPL	3-UPL	4-UPL	3-FACU				English Ivy
Hedychium coronarium					4-FAC								White Ginger-Lily
Hedychium flavescens			3-FAC							3-FAC			Cream Ginger-Lily
Hedysarum alpinum								3-FAC					Alpine Sweet-Vetch
Helenium amarum										2-FACU			Yellowdicks

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Helenium microcephalum					2-FACW								Small-Head Sneezeweed
Helenium vernale					3-FACW								Savannah Sneezeweed
Helianthus floridanus					3-FACW								Florida Sunflower
Helianthus heterophyllus			2-OBL			2-OBL							Variable-Leaf Sunflower
Helianthus microcephalus						4-UPL							Small Woodland Sunflower
Helianthus nuttallii		2-FACW			2-FACW								Nuttall's Sunflower
Helianthus strumosus		4-UPL				3-FACU		3-FACU	3-FACU				Pale-Leaf Woodland Sunflower
Heloscradium nodiflorum					2-OBL				2-OBL				Fool's-Watercress
Heracleum mantegazzianum		2-FAC			2-FAC					2-FAC			Giant Hogweed
Hexastylis sorrei	New	4-FACW			3-FACW								Sandhills Heartleaf
Hieracium greenii		2-FACU											Green's Hawkweed
Hippuris lanceolata	New										3-OBL		Panarctic Mare's-Tail
Hordeum depressum		2-FACW											Dwarf Barley
Houstonia caerulea						3-FACU							Quaker-Ladies
Houttuynia cordata						2-FAC							Chameleon
Hydrilla verticillata				2-OBL				2-OBL					Water-Thyme
Hydrocharis morsus-ranae		2-OBL			2-OBL								Common Frogbit
Hymenocallis crassifolia					3-OBL								Coastal Carolina Spider-Lily
Hyparrhenia rufa						4-FACU							Jaragua
Hypericum canadense						2-FACW							Lesser Canadian St. John's-Wort
Hypericum erythraeae	New	4-OBL											Georgia St. John's-Wort
Hypericum nudiflorum								2-FACW					Early St. John's-Wort
Hypericum virgatum		4-FAC						4-FAC					Sharp-Leaf St. John's-Wort

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Hypericum walteri									2-OBL				Greater St. John's-Wort
Hypoxis curtissii						2-FACW							Curtiss' Yellow Star-Grass
Hypoxis juncea					3-FACW								Fringed Yellow Star-Grass
Ilex aquifolium		4-FACU	3-FACU				4-FACU		3-FACU				English Holly
Ilex montana		4-FAC							3-FACU				Mountain Holly
Illicium parviflorum					4-FACW								Yellow Anisetree
Impatiens aurella						2-FACW							Pale-Yellow Touch-Me-Not
Impatiens balsamina						4-UPL							Garden-Balsam
Imperata cylindrica						3-FACU				3-FACU			Cogon Grass
Indigofera suffruticosa					4-UPL								Anil-de-Pasto
Ipomoea alba								3-FAC					Tropical White Morning-Glory
Ipomoea cairica										3-FACU			Mile-a-Minute-Vine
Ipomoea hederifolia					3-FAC								Scarlet-Creeper
Ipomoea indica					4-FAC					3-FAC			Ocean-Blue Morning-Glory
Ipomoea quamoclit										3-FACU			Cypress-Vine
Ipomoea violacea			3-FAC			3-FAC							Heavenly-Blue Morning-Glory
Iresine diffusa			3-FAC										Juba's-Bush
Iris fulva									2-OBL				Copper Iris
Iris giganticaerulea			3-OBL			3-OBL							Giant Blue Iris
Iris X nelsonii	New	3-OBL											[*brevicaulis* X *fulva* X *hexagona*]
Isoetes flettii										3-OBL			Flett's Quillwort
Isoetes novae-angliae	New								3-OBL				New England Quillwort
Isoetes occidentalis						2-OBL							Western Quillwort
Isoetes texana	New	3-OBL											Coastal Bend Quillwort
Isoetes tuckermanii		2-OBL											Tuckerman's Quillwort
Isoetes X altonharvillii		3-OBL											[*engelmannii* X *valida*]

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Isoetes X brittonii		2-OBL											[*engelmannii X riparia*]
Isoetes X carltaylori	New	3-OBL			4-OBL								[*acadiensis X engelmannii*]
Isoetes X eatonii		2-OBL											[*echinospora X engelmannii*]
Isoetes X echtuckeri	New								3-OBL				[*echinospora X tuckermannii*]
Isoetes X fairbrothersii		3-OBL							3-OBL				[*engelmannii X lacustris*]
Isoetes X truncata										3-OBL			[*flettii X maritima*]
Jaegeria hirta	New		4-FACU										Botao-de-Ouro
Juncus anthelatus		2-FACW	2-FACW		2-FACW	2-FACW				2-FACW			Kentucky Rush
Juncus bulbosus									3-OBL				Bulbous Rush
Juncus compressus		3-FACW			3-FACW								Round-Fruit Rush
Juncus elliottii			3-FACW										Elliott's Rush
Juncus ensifolius								2-FACW					Dagger-Leaf Rush
Juncus pallidus	New	3-FACW			4-OBL								Javelin-Grass
Juncus paludosus	New	4-OBL											Florida Rush
Juncus pylaei						2-OBL							Common Rush
Juncus saximontanus											2-FACW		Rocky Mountain Rush
Juncus vaseyi					2-FACW								Vasey's Rush
Justicia americana			2-OBL										American Water-Willow
Justicia crassifolia					3-OBL								Thick-Leaf Water-Willow
Krigia caespitosa									3-FACU				Weedy Dwarf-Dandelion
Lantana urticoides										3-FACU			West Indian Shrub-Verbena
Leitneria pilosa	New	4-FACW			4-FACW								Hairy Corkwood
Lepidium latifolium		4-FAC			3-FAC								Broad-Leaf Pepperwort
Lepidium nitidum						2-FAC			2-FAC				Shining Pepperwort
Leucothoe axillaris									2-FACW				Coastal Doghobble

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Leucothoe fontanesiana								2-FACW					Highland Doghobble
Leymus condensatus						2-FACU							Giant Lyme Grass
Limnobium spongia			2-OBL							2-OBL			American Spongeplant
Limnosciadium pumilum					4-OBL								Prairie Dogshade
Limonium binervosum	New		3-FAC										Rock Sea-Lavender
Lindernia procumbens									2-FACW				Prostrate False Pimpernel
Linum floridanum									2-FAC				Florida Yellow Flax
Linum intercursum		4-FACU			3-FACU			3-FACU					Sandplain Flax
Linum virginianum						4-FAC							Woodland Flax
Liquidambar styraciflua										3-FAC			Sweet-Gum
Lonicera caurlana						2-FAC							Sweet-Berry Honeysuckle
Lonicera japonica		4-FACU											Japanese Honeysuckle
Ludwigia bonariensis					3-OBL								Carolina Primrose-Willow
Ludwigia octovalvis			2-OBL		2-OBL								Mexican Primrose-Willow
Lupinus polyphyllus		3-FAC			4-FAC								Blue-Pod Lupine
Luzula arcuata						3-FACU							Curved Wood-Rush
Lycium torreyi						3-FAC				3-FACU			Squawthorn
Lycopodiella margueritae					3-FACW			3-FACW					Prostrate Club-Moss
Lycopodiella subappressa								3-FACW					Northern Appressed Club-Moss
Lycopus americanus											2-OBL		Cut-Leaf Water-Horehound
Lycopus rubellus										2-OBL			Taper-Leaf Water-Horehound
Lycopus X sherardii						2-OBL							[*uniflorus* X *virginicus*]
Lysimachia maritima					4-FAC								Sea-Milkwort
Lysimachia punctata			2-OBL										Large Yellow-Loosestrife
Lythrum salicaria											3-OBL		Purple Loosestrife
Macroptilium lathyroides					2-FACU								Wild Bush-Bean

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Madia glomerata		4-FACU			3-FACU								Mountain Tarplant
Magnolia acuminata		3-FACU				3-FACU		3-FACU	3-FACU				Cucumber-Tree
Magnolia asheri					3-FACU								Ashe's Magnolia
Mahonia nervosa		4-FACU	3-FACU		3-FACU								Cascade Oregon-Grape
Marsilea drummondii	New		3-OBL										Drummond's Water-Clover
Marsilea mutica						2-OBL		2-OBL					Australian Water-Clover
Marsilea vestita									2-OBL				Hairy Water-Clover
Medeola virginiana		4-FACU			3-FAC				4-FACU				Indian Cucumber-Root
Meehania cordata								3-FACU	3-FACU				Meehan's-Mint
Melaleuca citrina			2-UPL							2-UPL			Crimson-Bottlebrush
Melanthera angustifolia	New	4-FAC											Everglades Squarestem
Melia azedarach									3-FACU				China-Berry
Melica bulbosa						9-RST		2-FACU					Onion Grass
Melilotus indicus								3-FACU					Indian Sweet-Clover
Melochia corchorifolia						4-FAC			3-FACU				Chocolate-Weed
Mentha aquatica						3-FACW							Water Mint
Mentha X gracilis			4-FACW							3-FACW			[*arvensis* X *spicata*]
Mentha X rotundifolia		4-FAC	4-FAC			4-FAC		4-FAC	4-FAC	3-FAC			[*spicata* X *suaveolens*]
Mesembryanthemum cordifolium										2-FAC			Heart-Leaf Iceplant
Mesembryanthemum crystallinum										3-FACU			Crystalline Iceplant
Mesembryanthemum nodiflorum		2-FAC											Slender-Leaf Iceplant
Micranthes fragosa	New		3-FACW							3-FACW			Cliff Pseudosaxifrage
Micranthes palmeri						4-FAC							Palmer's Pseudosaxifrage

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Micranthes petiolaris		3-FACW											Michaux's Pseudosaxifrage
Milium effusum						2-FACU			2-FACU				American Millet Grass
Mimosa pudica					2-FACU								Shameplant
Mimosa strigillosa					2-FAC			2-FAC					Powderpuff
Mimulus breviflorus						2-FACW							Short-Flower Monkey-Flower
Mimulus guttatus		2-OBL											Seep Monkey-Flower
Mimulus washingtonensis						2-OBL							Washington Monkey-Flower
Moehringia macrophylla	New		3-FAC			4-UPL			3-FACU	3-FACU			Large-Leaf Grove-Sandwort
Molinia caerulea					2-FACU								Purple Moor Grass
Momordica charantia			3-FACU			3-FACU			3-FACU				Balsam-Pear
Monarda clinopodia		2-FACU							2-FACU				White Bergamot
Morinda umbellata	New	4-FACU											Cheeseshrub
Morus rubra			2-FACU							2-FACU			Red Mulberry
Muhlenbergia expansa						2-FACW							Spreading Muhly
Muhlenbergia filiformis		2-FACW						2-FACW					Pullup Muhly
Muhlenbergia glabriflora		3-FAC			4-FAC	4-FAC			3-FAC				Smooth Muhly
Muhlenbergia tenuiflora		3-FACU				3-FACU		3-FACU	3-FACU				Slim-Flower Muhly
Muhlenbergia uniflora			2-OBL			2-OBL							Bog Muhly
Myosotis sylvatica											3-UPL		Woodland Forget-Me-Not
Myriophyllum heterophyllum										2-OBL			Two-Leaf Water-Milfoil
Myriophyllum humile						2-OBL							Low Water-Milfoil
Myriophyllum pinnatum										2-OBL			Cut-Leaf Water-Milfoil
Nama jamaicense					4-FACW								Jamaican-Weed
Navarretia fossalis										3-OBL			Vernal-Pool Pincushion-Plant
Navarretia prostrata										3-OBL			Prostrate Pincushion-Plant

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Nelsonia canescens		3-FAC											Blue Pussyleaf
Nelumbo nucifera						2-OBL							Sacred Lotus
Neptunia oleracea		3-OBL			4-FACW								Garden Puff
Nicotiana obtusifolia					2-FACU								Desert Tobacco
Nicotiana plumbaginifolia					2-FAC								Tex-Mex Tobacco
Nicotiana tabacum						3-UPL							Cultivated Tobacco
Nuphar sagittifolia									2-OBL				unknown
Nyssa ogeche					3-OBL								Ogeechee Tupelo
Oenanthe javanica									2-OBL				Water-Celery
Oenothera canescens		2-FAC	2-FAC										Spotted Evening-Primrose
Oenothera elata								3-FACW					Hooker's Evening-Primrose
Oenothera flava		4-FACU											Long-Tube Evening-Primrose
Oenothera jamesii		2-FACW											Trumpet Evening-Primrose
Ophioglossum petiolatum						4-FACW							Long-Stem Adder's-Tongue
Oplismenus hirtellus								3-FACU					Long-Leaf Basket Grass
Oplopanax horridus						4-FACU							Devil's-Club
Ornithogalum caudatum					3-FACU								False Sea-Onion
Orobanche riparia		2-FACW			2-FACW			2-FACW		2-FACW			River Broom-Rape
Osmorhiza berteroi								2-FACU					Mountain Sweet-Cicely
Oxalis corniculata											3-FACU		Creeping Yellow Wood-Sorrel
Oxytropis czukotica	New										3-UPL		Amphi-Beringian Locoweed
Packera pseudaurea					2-FACW								Streambank Groundsel
Palhinhaea cernua					3-FAC								Monkey's Paw
Parnassia parviflora											2-OBL		Small-Flower Grass-of-Parnassus
Paspalum denticulatum					2-OBL								Pull-and-Be-Damned
Paspalum floridanum									2-FACW				Florida Crown Grass

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Paspalum notatum								3-FACU					Bahia Grass
Paspalum orbiculatum		4-FAC			4-FAC								Circular Crown Grass
Paspalum virgatum							2-FACW						Talquezal
Passiflora foetida					3-FAC								Scarlet-Fruit Passion-Flower
Paulownia tomentosa			4-UPL										Princesstree
Paxistima myrsinites			3-FACU			3-FACU							Oregon Boxleaf
Perideridia parishii						2-FAC							Parish's Yampah
Perilla frutescens		4-FACU			3-FACU	3-FAC			3-FAC	3-UPL			Beefsteakplant
Persea palustris						2-FACW							Swamp Bay
Persicaria arifolia			2-OBL							2-OBL			Halberd-Leaf Tearthumb
Persicaria longiseta		2-FAC			2-FAC								Bristly Lady's-Thumb
Persicaria meisnenana					4-FAC								Branched Tearthumb
Persicaria minor		2-OBL											Pygmy Smartweed
Persicaria perfoliata										2-FAC			Asiatic Tearthumb
Persicaria puritanorum	New								4-FACW				Puritan Smartweed
Persicaria robustior			3-OBL			3-OBL							Stout Smartweed
Persicaria wallichii					2-FAC				2-FAC				Garden Smartweed
Petasites frigidus		3-FACW											Arctic Sweet-Colt's-Foot
Phacelia covillei								2-FACW					Buttercup Scorpion-Weed
Phacelia viscida									3-UPL				Tacky Scorpion-Weed
Phalaris aquatica						3-FAC							Harding Grass
Phalaris paradoxa									3-FAC				Mediterranean Canary Grass
Phegopteris hexagonoptera						4-FAC							Broad Beech Fern
Phragmites karka		3-FACW	3-OBL			4-FACU				3-FAC			Tropical Reed
Phyla cuneifolia					4-FAC								Wedgeleaf
Phyllanthus carolinensis									2-FAC				Carolina Leaf-Flower
Phyllanthus fluitans	New	3-OBL											Red Root Floater

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Phyllostachys nigra		2-FACU				2-FACU							Black Bamboo
Physalis minima					2-FACU			2-FACU					Pygmy Ground-Cherry
Physostegia angustifolia									3-FACW				Narrow-Leaf False Dragonhead
Phytolacca icosandra		3-FAC	4-FACU	4-FACU	4-FACU								Tropical Pokeweed
Picea pungens		3-FAC											Blue Spruce
Pimpinella saxifraga	New	4-UPL			3-FACU			3-UPL	3-FACU	3-UPL			Solid-Stem Burnet-Saxifrage
Pinckneya bracteata					3-FACW								Fevertree
Pinguicula planifolia					4-OBL								Chapman's Butterwort
Pinus ponderosa									3-UPL				Ponderosa Pine
Plagiobothrys leptocladus								3-FACW					Alkali Popcorn-Flower
Plagiobothrys nitens	New		4-OBL							3-FACW			Shiny-Nutlet Popcorn-Flower
Plagiobothrys reticulatus									2-FACW				Netted Popcorn-Flower
Plantago pusilla			3-FAC							3-FACU			Dwarf Plantain
Platanthera aquilonis					3-FACW	3-OBL		3-FACW	3-FACW		3-FACW		Bog Orchid
Platanthera brevifolia						4-FACU				3-FACU			Short-Leaf Fringed Orchid
Platanthera grandiflora								2-FACW					Greater Purple Fringed Orchid
Platanthera huronensis		3-OBL											Lake Huron Green Orchid
Platanthera shriveri	New				4-FAC								Shriver's Fringed Orchid
Platanthera X beckneri	New	3-FACW											[*conspicua* X *cristata*]
Platanthera X enigma	New								3-FACW				[*grandiflora* X *psycodes*]

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Platanthera X estesii	New		3-FACW							3-FAC			[*dilatata* X *stricta*]
Platanthera X folsomii	New		3-FACW							3-FAC			[*dilatata* X *yosemitensis*]
Platanthera X kelleyi	New		3-FACW							3-FAC			[*sparsiflora* X *tescamnis*]
Platanthera X lueri	New	3-FACW											[*conspicua* X *ciliaris*]
Platanthera X smithii	New					3-FAC				3-FAC			[*aquilonis* X *tescamnis*]
Platanthera yosemitensis	New		3-FACW							3-FACW			Yosemite Bog Orchid
Plecostachys serpyllifolia	New		3-FACU										Petite-Licorice
Pleea tenuifolia					3-OBL								Rush-Featherling
Pleopeltis polypodioides									4-UPL				Resurrection Fern
Pluchea baccharis						2-FACW							Rosy Camphorweed
Plumbago auriculata					3-UPL								Cape Leadwort
Poa arctostepporum	New										3-UPL		Amphi-Beringian Blue Grass
Poa bulbosa	New	3-FACU	3-FACU		3-FACU	3-FACU		3-FACU	3-FACU	3-FACU			Bulbous Blue Grass
Poa nemoralis						3-FACU							Forest Blue Grass
Poa secunda		2-FACU			2-FACU								Curly Blue Grass
Polemonium caeruleum		2-FACW						2-FACW					Charity
Polemonium longii	New				3-FACU								Long's Jacob's-Ladder
Polemonium micranthum						2-FACU							Annual Jacob's-Ladder
Polygala ambigua			2-FACU			2-FACU							Alternate Milkwort
Polygala brevifolia					3-FACW								Little-Leaf Milkwort
Polygala hookeri					3-FACW								Hooker's Milkwort
Polygala sanguinea			4-FACU										Purple Milkwort
Polygonatum pubescens		4-FACU				4-FACU		3-FACU	3-FACU				Hairy Solomon's-Seal

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Polygonum achoreum		4-FAC											Leathery Knotweed
Polygonum argyrocoleon					4-OBL			4-OBL	3-FAC				Silver-Sheath Knotweed
Polygonum douglasii		4-FACU											Douglas' Knotweed
Polygonum patulum						4-FACW			3-FACU				Bellard's Knotweed
Polygonum plebeium	New	4-FACW											Common Knotweed
Polygonum rail	New								3-FAC				Ray's Knotweed
Polypogon interruptus					3-FACW			3-FACW					Ditch Rabbit's-Foot Grass
Polypogon viridis					4-FACW								Beardless Rabbit's-Foot Grass
Polystichum munitum					2-FACU				2-FACU				Pineland Sword Fern
Pontederia cordata			2-OBL										Pickerelweed
Pontederia rotundifolia	New	3-OBL											Tropical Pickerelweed
Portulaca grandiflora			3-UPL							3-UPL			Rose-Moss
Potamogeton friesii		2-OBL											Flat-Stalk Pondweed
Potamogeton oblongus	New	3-OBL			3-OBL				3-OBL				Cinnamon-Spot Pondweed
Potamogeton tennesseensis		2-OBL											Tennessee Pondweed
Potamogeton X absconditus	New								3-OBL				[*perfoliatus* X *richardsonii*]
Potamogeton X aemulans	New								3-OBL				[*bicupulatus* X *epihydrus*]
Potamogeton X faxonii		2-OBL	2-OBL		2-OBL	2-OBL							[*illinoensis* X *nodosus*]
Potamogeton X hagstroemii										2-OBL			[*gramineus* X *richardsonii*]
Potamogeton X mirabilis	New								3-OBL				[*gramineus* X *oakesianus*]
Potamogeton X nericus			3-OBL			3-OBL		3-OBL		3-OBL			[*alpinus* X *gramineus*]
Potamogeton X nitens					3-OBL								[*gramineus* X *perfoliatus*]
Potamogeton X rectifolius					2-OBL					2-OBL			[*nodosus* X *richardsonii*]
Potamogeton X sparganiifolius	New				3-OBL				3-OBL				[*gramineus* X *natans*]
Potamogeton X spathuliformis			2-OBL			2-OBL				2-OBL			[*gramineus* X *illinoensis*]
Potamogeton X subdentatus	New	3-OBL							3-OBL				[*illinoensis* X *perfoliatus*]

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Potamogeton X subobtusus	New								3-OBL				[*alpinus* X *nodosus*]
Potamogeton X undulatus	New							3-OBL	3-OBL				[*praelongus* X *crispus*]
Potamogeton X versicolor	New								3-OBL				[*epihydrus* X *perfoliatus*]
Potentilla litoralis	New								3-FACU				Coastal Cinquefoil
Potentilla pensylvanica					2-FACU								Pennsylvania Cinquefoil
Potentilla plattensis								2-FACW					Platte River Cinquefoil
Potentilla uliginosa	New		4-OBL							3-FACW			Cunningham Marsh Cinquefoil
Praxelis clematidea	New	3-FACU											Praxelis
Proboscidea louisiana							4-FACW						Ram's-Horn
Prunus avium		4-UPL	3-FACU		4-UPL	4-UPL		3-FACU	3-FACU				Sweet Cherry
Pseuderanthemum variabile					4-FACU								Night-and-Afternoon
Pseudognaphalium canescens					3-FACU								Wright's Rabbit-Tobacco
Pseudotsuga menziesii		2-FACU			2-FACU								Douglas-Fir
Pteris irregularis				4-UPL									Zigzag Brake
Puccinellia lemmonii						3-FACW							Lemmon's Alkali Grass
Puccinellia lucida			3-OBL										Shining Alkali Grass
Puccinellia nutkaensis		4-FACW			3-FACW								Nootka Alkali Grass
Puccinellia tenella					4-FACW								Tundra Alkali Grass
Pueraria montana			3-UPL										Kudzu
Pyrola asarifolia		3-FAC			4-FAC								Pink Wintergreen
Pyrrocoma lanceolata		4-FAC											Lance-Leaf Goldenweed
Quercus hemisphaenica			3-FACU										Darlington's Oak
Quercus pagoda									4-FACW				Cherry-Bark Oak

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Quercus rubra			2-FACU										Northern Red Oak
Quercus similis					2-FACW								Bottom-Land Post Oak
Quercus X macnabiana								2-FACU					[*sinuata X stellata*]
Ranunculus muricatus								3-FACW					Spiny-Fruit Buttercup
Ranunculus platensis						2-FAC							Prairie Buttercup
Ranunculus subrigidus											2-OBL		Short-Beak Water-Crowfoot
Ranunculus sulphureus			3-FACW			3-OBL				3-FACW			Sulphur Buttercup
Ranunculus trifobus					3-FAC								Three-Lobe Buttercup
Reynoutria X bohemica		3-FACU	3-FACU		3-FACU	4-FACU		4-FACU	3-FACU		3-FACU		[*japonica X sachalinensis*]
Rhamnus alaternus	New		3-FACU										Evergreen Buckthorn
Rhamnus alnifolia		4-FAC											Alder-Leaf Buckthorn
Rhinanthus minor								3-FACU					Little Yellow-Rattle
Rhizophora mangle					2-OBL								Red Mangrove
Rhododendron macrophyllum			3-FACU										California Rhododendron
Rhododendron prinophyllum			2-FAC			2-FAC							Early Azalea
Rhus copallinum			3-FACU										Winged Sumac
Rhynchospora brachychaeta			3-FACW			3-OBL							West Indian Beak Sedge
Rhynchospora caduca								3-OBL					Angle-Stem Beak Sedge
Rhynchospora careyana									2-OBL				Broad-Fruit Horned Beak Sedge
Rhynchospora inundata						2-OBL							Narrow-Fruit Horned Beak Sedge
Rhynchospora latifolia								3-FACW					Sand-Swamp Whitetop
Rhynchospora odorata					2-OBL								Fragrant Beak Sedge
Rhynchospora rariflora								2-OBL					Few-Flower Beak Sedge

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Rhynchospora recognita		3-FACW	3-FACW	4-FACW		3-FACW	4-FACW	3-FACW	3-FACW	3-FACW			Coarse Globe Beak Sedge
Ribes glandulosum		3-FACW											Skunk Currant
Ribes laxiflorum			4-FACU			3-FACU					3-FACU		Trailing Black Currant
Ribes lobbii			3-FACU										Oregon Gooseberry
Ribes sanguineum			4-UPL										Blood Currant
Rorippa curvipes		3-FACW											Blunt-Leaf Yellowcress
Rorippa dubia		3-FACW	3-FAC							3-FACW			unknown
Rorippa sessiliflora										2-OBL			Stalkless Yellowcress
Rousseila humilis		3-FACU											Shineseed
Rubus apogaeus					4-FAC								Falling Dewberry
Rubus arizonensis		2-FACU											Arizona Dewberry
Rubus baileyanus						2-FACU							Bailey's Dewberry
Rubus caesius					3-FACU			3-FACU					European Dewberry
Rubus floricomus	New	4-FAC			4-FAC				3-FAC				Many-Flower Blackberry
Rubus hispidoides	New								3-FACW				Bog Dewberry
Rubus hypolasius					4-FAC								Pineland Dewberry
Rubus inclinis	New				4-FACW				4-FACW				Marshland Blackberry
Rubus lawrencei	New	3-FAC			3-FAC				4-FAC				Adirondack Blackberry
Rubus longii									2-FAC				Long's Blackberry
Rubus missouricus		2-FACU											Missouri Dewberry
Rubus multiformis					2-FAC								Variable Blackberry
Rubus paganus									3-FACW				St. Lawrence Dewberry

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Rubus paludivagus	New								4-FAC				Cape Cod Blackberry
Rubus parviflorus		3-FACU			3-FACU								Western Thimble-Berry
Rubus pedatus						4-FAC							Strawberry-Leaf Raspberry
Rubus pensilvanicus			3-FAC							3-FAC			Pennsylvania Blackberry
Rubus phoenicolasius		3-FACU	3-FACU		3-FACU			3-FACU		3-FAC			Wine Raspberry
Rubus plus					4-FACU			3-FAC					Hairy-Leaf Dewberry
Rubus probabilis					4-FACU								Tree Blackberry
Rubus sons					3-FAC								New Orleans Dewberry
Rubus suus						4-FAC							Branched Blackberry
Rubus tardatus		4-FACU			3-FAC			3-FAC					Wet-Thicket Dewberry
Rudbeckia nitida					4-FAC								Shiny Coneflower
Rudbeckia occidentalis						2-FAC							Western Coneflower
Rumex floridanus					3-FACW				3-FACW				Florida Dock
Rumex hesperus	New		4-FACW							3-FACW			Western Willow dock
Rumex kerneri										3-FACW			Kerner's Dock
Rumex lapponicus			4-FAC			3-FAC				3-UPL			Lapland Sorrel
Rumex maritimus	New	3-FACW			4-FAC				3-FACW				Golden Dock
Rumex mexicanus						3-FAC			4-FACW	3-FAC			Mexican Dock
Rumex occidentalis		3-OBL			4-OBL								Western Dock
Rumex palustris	New		4-FACW							3-FAC			Marsh Dock
Rumex persicarioides		2-FACW			2-FACW					2-FACW			Coastal Dock
Rumex stenophyllus		2-FACW											Narrow-Leaf Dock
Rumex violascens									2-FACW				Violet Dock
Sabal minor								2-FACW					Dwarf Palmetto

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Sabatia campanulata						2-FACW							Slender Rose-Gentian
Sabatia kennedyana					2-OBL								Plymouth Rose-Gentian
Sacciolepis indica					4-FACW								Glenwood Grass
Sagina procumbens						3-FACW							Bird-Eye Pearlwort
Sagittaria ambigua									2-OBL				Kansas Arrowhead
Sagittaria cuneata		2-OBL											Arum-Leaf Arrowhead
Salix atrocinerea		2-FACW				2-FACW		2-FACW					Smooth-Twig Gray Willow
Salix caprea			3-FACW							3-FACW			Goat Willow
Salix cinerea						2-FACW				2-FACW			Large Gray Willow
Salix elaeagnos		4-FAC			3-FACW			3-FACW					Elaeagnus Willow
Salix famelica					2-FACW								unknown
Salix myrsinifolia	New								3-OBL				Dark-Leaf Willow
Salix nigra			4-OBL										Black Willow
Salix triandra	New	4-OBL			3-FACW			3-FACW	3-FACW				Almond-Leaf Willow
Salix viminalis								3-FACW					Basket Willow
Salix X glatfelteri	New	4-FACW			3-FACW			3-FACW	3-FACW				[*amygdaloides* X *nigra*]
Salvinia molesta				2-OBL						2-OBL			Kariba-Weed
Salvinia oblongifolia	New		3-OBL										Oblong-Leaf Water-Moss
Samanea saman													Raintree
Sarcocornia ambigua					2-OBL	2-OBL							Chickenclaws
Sarcocornia utahensis		3-OBL											Utah Swampfire
Sarracenia flava									2-OBL				Yellow Pitcherplant
Sarracenia leucophylla					3-OBL					3-OBL			White-Top Pitcherplant
Sarracenia minor					3-OBL								Hooded Pitcherplant
Sarracenia rosea					3-OBL								Rosy Pitcherplant

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Saxifraga rivularis									3-FACW				Alpine-Brook Saxifrage
Sceptridium biternatum									2-FAC				Sparse-Lobe Grape Fern
Sceptridium oneidense		4-FAC						3-FAC	3-FAC				Blunt-Lobe Grape Fern
Schedonorus giganteus	New								3-FACU				Giant False Rye Grass
Schenkia spicata					2-FACW								Mediterranean Schenkia
Schinus molle		4-FACU		4-FACU		3-FACU	3-UPL			3-UPL			Peruvian Peppertree
Schoenolirion albiflorum					4-FACW								White Sunnybell
Schoenoplectus californicus								2-OBL					California Club-Rush
Schoenoplectus glaucus		2-OBL			2-OBL								Tuberous Club-Rush
Schoenoplectus heterochaetus		2-OBL											Pale Great Club-Rush
Schoenoplectus lacustris	New	3-OBL			3-OBL				3-OBL				Common Club-Rush
Scilla luciliae		3-FAC											Boissier's Glory-of-the-Snow
Scirpoides holoschoenus									2-OBL				Round-Head Club-Rush
Scirpus atrocinctus			3-OBL										Black-Girdle Bulrush
Scirpus atrovirens			2-OBL							2-OBL			Dark-Green Bulrush
Scleria oligantha									3-FAC				Little-Head Nut-Rush
Sedum ternatum		4-FACU						3-FACU	3-FACU				Woodland Stonecrop
Selaginella eclipes		3-FACW			3-FACW			3-FACW					Hidden Spike-Moss
Selaginella uncinata					3-OBL								Blue Spike-Moss
Senecio hydrophiloides						2-FACW							Stout Meadow Ragwort
Senecio minimus			3-FACU										Coastal Burnweed
Senecio pseudoarnica									3-FACU				Seaside Ragwort
Senna alata					3-FACU								Emperor's-Candlesticks
Sesbania herbacea										3-FACW			Peatree
Seymeria cassioides			2-FAC			2-FAC							Yaupon Black-Senna

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Shortia galacifolia									3-FACU				Oconee-Bells
Sibbaldia tridentata		2-FACU											Shrubby-Fivefingers
Sida acuta			3-UPL			4-UPL			3-FACU				Common-Wireweed
Sidalcea campestris			3-FACU										Meadow Checkerbloom
Sidalcea neomexicana		2-FACW											Rocky Mountain Checkerbloom
Silene uralensis						3-FACW							Apetalous Catchfly
Silphium integrifolium		3-FAC			3-FAC	3-FAC		3-FACU		3-FAC			Entire-Leaf Rosinweed
Silphium perfoliatum			3-FACW										Cup-Plant
Sinapis alba		3-FAC	4-FAC	4-FAC	3-FACW			3-FACU	3-FACU				White-Mustard
Sisyrinchium fuscatum								4-FACW					Coastal-Plain Blue-Eyed-Grass
Sisyrinchium sagittiferum					4-FACW								Spear-Bract Blue-Eyed-Grass
Sium carsonii	New	3-OBL			4-OBL				3-OBL				Carson's Water-Parsnip
Smilax glauca										3-FACU			Sawbrier
Smilax pulverulenta						3-FACU							Downy Carrion-Flower
Solandra grandiflora									3-FACU				Showy Chalicevine
Solanum nigrum									3-FACU				European Black Nightshade
Solanum torvum					3-FACU								Turkey-Berry
Solenostemon scutellarioides					2-FACU				2-FACU				Painted-Nettle
Solidago caesia						2-FACU							Wreath Goldenrod

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Solidago fistulosa									4-FACW				Pine-Barren Goldenrod
Solidago multiradiata					2-FACU				2-FACU				Rocky Mountain Goldenrod
Solidago stricta						3-OBL							Wand Goldenrod
Solidago X asperula		4-UPL											[*rugosa* X *sempervirens*]
Sophronanthe pilosa								3-FACW					Shaggy False Hedge-Nettle
Sparganium fluctuans		2-OBL											Floating Burr-Reed
Spergulana diandra						2-FACW							Alkali Sandspurry
Spergulana echinosperma			3-OBL										Bristle-Seed Sandspurry
Sphenopholis filiformis						3-FAC							Long-Leaf Wedgescale
Sphenopholis intermedia		2-FAC	2-FAC		2-FAC	2-FAC				2-FAC	2-FAC		Slender Wedgescale
Sphenopholis nitida		4-UPL			3-FAC	4-UPL			4-UPL				Shiny Wedgescale
Spinulum annotinum		3-FAC											Interrupted Club-Moss
Spiraea betulifolia								3-FAC					Shiny-Leaf Meadowsweet
Spiranthes odorata									2-OBL				Marsh Ladies'-Tresses
Sporobolus texanus		3-FAC			4-FACU								Texas Dropseed
Sporobolus virginicus					4-FAC								Seashore Dropseed
Sporobolus wrightii		4-FAC				3-FAC				3-FACW			Wright's Dropseed
Stachys appalachiana	New				4-OBL								Blue Ridge Hedge-Nettle
Stachys clingmanii									3-FACU				Clingman's Hedge-Nettle
Stachys crenata								3-FAC					Mouse's-Ear
Stellaria alsine			3-OBL										Bog Chickweed
Stellaria borealis		3-FACW											Boreal Starwort
Stellaria cuspidata					2-FAC								Mexican Starwort
Stenandrium dulce					3-FACW								Sweet Shaggytuft
Stuckenia filiformis		2-OBL											Slender-Leaf False Pondweed
Stuckenia X suecica	New							3-OBL	3-OBL				[*filiformis* X *pectinatus*]
Suaeda nigra		4-OBL											Shrubby Seepweed
Succisella inflexa	New				3-FACW				3-FACW				Frosted Pearls

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Suksdorfia violacea						2-FAC							Violet Mock Brookfoam
Symphoricarpos mollis			3-FACU										Creeping Snowberry
Symphoricarpos occidentalis		3-FAC											Western Snowberry
Symphyotrichum bahamense					2-OBL								Island American-Aster
Symphyotrichum ontarionis			2-FAC										Ontario American-Aster
Symphyotrichum squamatum						2-OBL							unknown
Symplocos tinctoria								2-FAC					Horsesugar
Tamarix gallica					4-FAC								French Tamarisk
Taraxacum ceratophorum									3-FAC				Horned Dandelion
Tarenaya hassleriana			4-FACU			3-FAC			3-FACU				Pinkqueen
Taxus brevifolia						2-FACU							Pacific Yew
Tillandsia recurvata							2-UPL			2-UPL			Small Ball-Moss
Tithonia diversifolia			3-FACU			4-FAC							Tree-Marigold
Tolmiea diplomenziesii	New		3-FAC							3-FACW			unknown
Toxicodendron diversilobum			4-FACU										Pacific Poison-Oak
Tradescantia virginiana						3-FAC							Virginia Spiderwort
Trematolobelia auriculata	New						4-FACW						Lanai False Lobelia
Trematolobelia kaalae	New						4-FACW						Waianae Mountains False Lobelia
Trematolobelia rockii	New						4-FACW						Molokai False Lobelia
Tribulus cistoides					4-UPL								Jamaican Feverplant
Trichomanes membranaceum		4-FACW											Scale-Edge Bristle Fern
Tridens albescens					3-FAC			3-FAC					White Fluff Grass
Trifolium depauperatum		3-FAC											Balloon Sack Clover
Triglochin scilloides						2-OBL							Flowering-Quillwort
Triodanis perfoliata							4-FACU						Clasping-Leaf Venus'-Looking-Glass
Triphasia trifolia			4-FACU			4-FACU							Limeberry

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Tropaeolum minus	New								3-FACU				Bush-Nasturtium
Tussilago farfara			2-FACU										Colt's-Foot
Typha X provincialis	New		3-OBL			3-OBL		3-OBL		3-OBL			[*domingensis* X *latifolia*]
Ulex europaeus		4-UPL	3-UPL		4-UPL		3-UPL		3-FACU				Common Gorse
Ulmus glabra		4-UPL	3-FACU		4-UPL	3-FACU		3-FACU					Wych Elm
Ulmus serotina						3-FACU							September Elm
Urochloa distachya					3-FACU	3-FAC							Tropical Liverseed Grass
Urochloa mutica										3-FACW			Para Liverseed Grass
Urochloa panicoides					2-FACU								Panic Liverseed Grass
Urochloa plantaginea									3-FAC				Plantain Liverseed Grass
Utricularia cornuta			2-OBL							2-OBL			Horned Bladderwort
Utricularia foliosa					2-OBL								Leafy Bladderwort
Utricularia inflata			2-OBL					2-OBL					Swollen Bladderwort
Utricularia ochroleuca						2-OBL		2-OBL					Dwarf Bladderwort
Utricularia striata			2-OBL			2-OBL							Striped Bladderwort
Vaccinium darrowii					4-FAC								Darrow's Blueberry
Vaccinium formosum									3-FACW				Southern Blueberry
Vaccinium X marianum									3-FACW				[*formosum* X *fuscatum* X *pallidum*]
Vachellia macracantha					4-FACU								Porknut
Valeriana uliginosa					3-OBL			3-OBL					Mountain Valerian
Valerianella chenopodiifolia	New	3-FAC			4-FAC			4-FAC	3-FAC				Goose-Foot Cornsalad
Verbena incompta	New	3-FACW	3-FACU		3-FACW	4-FAC	4-FAC	4-FAC		3-FAC			Brazilian Vervain
Verbena runyonii										2-FACW			Rio Grande Vervain
Verbena scabra								3-FACW					Sandpaper Vervain
Veronica cusickii						2-FAC							Cusick's Speedwell
Viburnum prunifolium										2-FACU			Smooth Blackhaw

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Vigna luteola									3-FACW				Wild Cow-Pea
Viola labradorica			3-FAC										Alpine Violet
Viola langloisii					2-FACW								Langlois' Violet
Viola pedatifida		4-FACU											Crow-Foot Violet
Viola X champlainensis	New				3-FAC				4-FACU				[*affinis* X *septentrionalis*]
Viola X dissita								2-FAC	2-FAC				[*hirsutula* X *palmata*]
Viola X greenmanii	New	3-FAC			4-FACU				3-FAC				[*cucullata* X *palmata*]
Viola X insessa	New								3-FACW				[*cucullata* X *nephrophylla*]
Viola X mistura	New	3-FAC			4-FACU			3-FACU	3-FACU				[*palmata* X *sagittata*]
Viola X napae		2-FAC											[*nephrophylla* X *sororia*]
Viola X subaffinis	New								3-FACW				[*affinis* X *nephrophylla*]
Viola X viarum									2-FACU				[*missouriensis* or *nephrophylla* X *pedatifida*]
Washingtonia robusta		4-FAC					4-FAC						Washington Fan Palm
Wolffia globosa								2-OBL	2-OBL				Asian Watermeal
X Achnella caduca								2-UPL					[*Achnatherum hymenoides* X *Nassella viridula*]
X Leydeum piperi	New		3-FAC							3-FAC			[*Hordeum jubatum* X *Leymus triticoides*]
Xerophyllum tenax			3-FACU			3-FAC					3-FACU		Western Turkeybeard
Xyris chapmanii					3-OBL								Chapman's Yellow-Eyed-Grass
Xyris louisianica					3-OBL								Louisiana Yellow-Eyed-Grass
Youngia japonica								3-FACU	3-FACU				Oriental False Hawk's-Beard
Zeltnera beyrichii			2-FACU										Quinineweed
Zeltnera calycosa										2-FACW			Buckley's Mountain-Pink

Scientific Name	New?	AGCP	AW	CB	EMP	GP	HI	MW	NCNE	WMVC	AK	SPI	Common Name
Ziziphus mauritiana							4-FACU			3-UPL			Indian Jujube
Zostera marina					2-OBL								Seawrack

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TWO NEW SPECIES OF *LYCIANTHES* SERIES *TRICOLORES* FROM EASTERN MEXICO

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ABSTRACT

Two new species, **Lycianthes venturana** E. Dean, **sp. nov.** and **Lycianthes michaelneei** E. Dean, **sp. nov.**, are described from eastern Mexico, the former from the state of Puebla and the latter from the state of Veracruz. Both species belong to series *Tricolores* Bitter, which is made up of six species of shrubs with simple trichomes and that are distributed from Nicaragua to western Mexico.

Lycianthes (Dun.) Hassler (Solanaceae) has both Old World and New World representatives and includes 150 to 200 species (Hunziker 2001). Its center of distribution, and the majority of its taxa, are found in the New World (from Mexico to Argentina), with ca. 30 taxa native to Mexico (ca. 14 endemic, two of them described here). The genus is the closest relative of the chile pepper genus *Capsicum* L. (Walsh & Hoot 2001; Bohs & Olmstead 1997), a relationship that was first pointed out by the German botanist Georg Bitter (Bitter 1919). The two genera have a similar calyx morphology, with the five lobes of the calyx truncated into a sleeve, below which may protrude five to ten appendages (commonly called calyx teeth). However, while *Capsicum* species have anthers that dehisce by longitudinal slits, the species of *Lycianthes* typically have poricidal anther dehiscence.

The entire genus was last monographed in 1919 by Bitter, who divided the species into sections and series but provided no identification key (Bitter 1919). In that work, he placed just two species, *Lycianthes tricolor* (Dun.) Bitter and *L. arrazolensis* (J.M. Coult. & Donn. Sm.) Bitter, in series *Tricolores* Bitter, a group of Mexican and Central American shrubs with simple trichomes and green, glandular markings on the corolla near the filament insertion point. During a study of herbarium specimens in preparation for a taxonomic treatment of series *Tricolores*, two things became clear.

First, not all members of the series have the distinctive green glands on the corolla.

Second, two Mexican taxa need to be described and published. An identification key to all six species will be included in the full treatment.

Terminology here follows that of previous papers on this genus (Dean 1998, 2007). Corolla, calyx, and pedicel measurements were made on mature flowers that appear to have opened for at least one day. Based on how the flowers look on the herbarium specimens, I am assuming that these two species are similar to other species in the series in having corollas that open and close each day for several days in a row.

LYCIANTHES VENTURANA E. Dean, **sp. nov. TYPE: MEXICO. Puebla.** Mpio. Teziutlán: Agua de Obispo, bosque de encino en cañada, 1350 m, 25 Nov 1976, *F. Ventura A. 13635* (holotype: MEXU). Figure 1.

Belonging to series *Tricolores* and differing from the other species of the series in having an apiculate tip to the berry that forms where the style abscises from the developing fruit. Most similar

Figure 1. Holotype of *Lycianthes venturana*.

to *Lycianthes jalicensis* in having nearly glabrous calyces and flowers, differing from that species in geographic distribution, calyx length usually less than or equal to 2 mm (usually 2.5–4 mm in *L. jalicensis*), curved style (usually straight in *L. jalicensis*), anther pores on shorter stamens dehiscing upwards or toward style (versus away from the style in *L. jalicensis*), and apiculate fruit (non-apiculate in *L. jalicensis*).

Shrub, 1–1.8 m high. **Indument** of tan, appressed-antrorse to slightly spreading one- to several-celled non-glandular trichomes. **Stems** olive-green to light brown when young, darker brown and woody with age, upper branching mostly unichasial with a few dichasial branching points, the longest sympodia 4.5–8.7 cm long, 1.25–3 mm diam., glabrous to pubescent with appressed trichomes to 1 mm long. **Leaves of upper sympodia** mostly geminate, sometimes unifoliate; largest leaves with petiole 4–15 mm long, the lamina ovate, elliptic, or obovate, 8.7–13.3 cm long, 3.7–6.5 cm wide, the tip acuminate, the base cuneate to attenuate, sometimes oblique, the margin entire to undulate, the lamina glabrous to puberulent with appressed trichomes to 1.25 mm long, densest along the veins; smaller geminate leaves similar but with petiole 2–5 mm long, the lamina ovate to elliptic, 4–8.5 cm long, 1.9–4.9 cm wide, the tip acuminate, the base cuneate. **Flowers** in groups of 1–6(–10) in the leaf axils with one or two flowers per group open at the same time, the pedicels at maturity erect, curved at the tip, (1.3–)1.4–2.8 cm long, nearly glabrous, the trichomes appressed-antrorse, 0.25–0.75 mm long; calyx urceolate to campanulate, 1.5–2(–2.5) mm long, 1.75–2.5 mm diam., nearly glabrous, the scarce trichomes 0.15–0.75 mm long, the calyx margin entire, the 10 appendages 1–3.5 mm long, 0.25–0.75 mm diam.; corolla campanulate, sometimes becoming rotate due to tearing, (5–)9–14 mm long, white, most likely greenish on abaxial side near main veins, nearly glabrous, tiny hairs < 0.1 mm long located on abaxial side near main veins; stamens with straight filaments of unequal length, the four shorter filaments 1.25–1.5 mm long, the fifth 4–5 mm long, glabrous; anthers lanceolate, 3.5–4 mm long, the pores dehiscing toward the style; ovary ovoid to conical, glabrous, 1–1.5 mm long, the style 7–9 mm long, curved upwards at the tip, the stigma oblong-capitate, slightly bilobed. **Fruit** ovoid, apiculate, ca. 6 mm long, 4 mm diam. (perhaps immature in specimens cited here), mature color unknown, lacking sclerotic granules, the calyx in fruit often widening, becoming bowl-shaped, ca. 2 mm long, 4 mm wide, the pedicel in fruit 1.8–2.2 cm long. **Mature seeds** not seen.

Distribution and habitat. Mexico. Puebla. Elevation: 1250-1450 m. Vegetation types: oak forest, altered mesophytic forest. Habitats: shady canyons and mountainsides. Phenology: flowering May through November; mature fruits by November, probably before.

Additional specimens examined. **MEXICO. Puebla**. Mpio. Ahuacatlan, 4.5 km al SE de Ahuacatlan, brecha a Zapotitlan,1250 m, 24 May 1986, *Tenorio 11426* con Romero (MEXU); Mpio. Teziutlán, Puente Colorado, carretera Teziutlán - Tlapacoyan, 1450 m, 24 Jun 1970, *Ventura 1350* (MEXU, MO); Mpio. Hueytamalco, Rancho El Milagro, 1350 m, 27 May 1986, *Ventura 21982* (MEXU).

Lycianthes venturana is described here based on limited material from which mature fruit size and color, seed type, and corolla color and shape cannot be exactly known. Based on the available pressed material, the corolla is white and campanulate and probably has greenish coloration along the veins on the abaxial side. Whether or not the corolla has the small greenish glands present in some members of series *Tricolores* is not known, because they do not persist well on pressed material. The corolla shape appears to be campanulate, but with expansion, the corolla may tear to allow it to open into a more rotate orientation. The fruits of the type specimen are dark in color, apiculate, 6 mm long and 4 mm wide. Whether these fruits are mature is not known. Because of the limited material available, I did not dissect these fruits to examine the seeds. The apiculate tip to the fruits forms from the remains of the base of the style. This feature is unique among the species of

series *Tricolores*. The specific epithet honors prolific Mexican plant collector Francisco Ventura Aburto. He collected most of the specimens upon which this species description is based between 1970 and 1986, and it only took 44 years for the species to be recognized as something new.

LYCIANTHES MICHAELNEEI E. Dean, **sp. nov. TYPE: MEXICO. Veracruz.** Mpio. Calcahualco: 4.2 km W of Escola on road to Jacal, 17.5 km by road NW of Coscomatepec, 19° 10' N, 97° 10'W, bosque de pino-encino, 2200 m, 12 Jan 1981, *M. Nee & G. Schatz 19791* (holotype: WIS; isotype: MEXU). Figure 2.

Most similar to *Lycianthes tricolor* in having notched seeds but differing from that species in geographic distribution, calyx teeth 0.5–1 mm diam. (versus 0.5 mm or less in *L. tricolor*), entirely purple flowers (versus white and purple in *L. tricolor*), largest leaves ca. 13.9–23.5 cm long (versus ca. 4–16 cm long in *L. tricolor*), matted hairs on the stem (unmatted, erect hairs in *L. tricolor*), and very long hairs on the leaves (to 2 mm long versus to 1.2 mm long in *L. tricolor*)

Shrub, 2–4 m high. **Indument** of light yellow erect to appressed, weak, one- to several-celled non-glandular trichomes. **Stems** tan to purplish, darker brown and woody with age, upper branching mostly unichasial with a few dichasial branching points, the longest sympodia 3–6.5 cm long, 1.25–4.5 mm diam., densely pubescent with matted trichomes to 1.2 mm long. **Leaves of upper sympodia** mostly geminate, sometimes unifoliate due to the smaller geminate leaf pair abscising early; largest leaves with petiole 17–35 mm long, lamina ovate, elliptic, or obovate, 13.9–23.5 cm long, 5.5–10.5 cm wide, the tip acuminate, the base rounded to cuneate, sometimes oblique, the margin entire to undulate, the lamina villous with erect to appressed trichomes to 2 mm long, spreading and very dense along the veins; smaller geminate leaves similar but with petiole 2–7 mm long, the lamina ovate to elliptic, 5.7–8.5 cm long, 2.6–4.7 cm wide, the tip acumintate, the base rounded to cuneate. **Flowers** in groups of 1–6(–10) in the leaf axils with one or two flowers per group open at the same time, the pedicels at maturity erect, curved at the tip, 1.5–2.8 cm long, densely pubescent, the trichomes weakly erect, 0.25–0.75(–1.2) mm long; calyx urceolate to campanulate, 2–3 mm long, 2.5–3.5 mm diam., densely pubescent, the trichomes 0.5–1 mm long, the calyx margin entire, the 10 appendages 1–4 mm long, 0.5–1 mm diam.; corolla rotate, 11–16 mm long, purple, most likely greenish purple on abaxial side, puberulent with tiny hairs < 0.2 mm long located on abaxial side near main veins; stamens with straight filaments of unequal length, the four shorter filaments 0.5–1 mm long, the fifth 3.5–4 mm long, glabrous; anthers lanceolate, 3–4 mm long, the pores of the anther of the longest stamen dehiscing toward the style, the pores of the anthers of the shorter stamens dehiscing away from the style; ovary round, glabrous, 1.5 mm long, the style 7–8.5 mm long, slightly curved to straight, the stigma very short, capitate, unlobed. **Fruit** round, 6–9 mm long, 6–8 mm diam., red at maturity, lacking sclerotic granules, the calyx in fruit widening, becoming bowl- to plate-shaped, 1.5–3 mm long, 5.5–9 mm wide, the pedicel in fruit 2.6–4.2 cm long. **Mature seeds** 20–30 in number, brown to orange, flattened, reniform, notched on one side, 2–3 mm long, 2–2.5 mm wide.

Distribution and habitat. Mexico. Veracruz. Elevation: 1750-2600 m. Vegetation types: oak-pine forest, deciduous forest (bosque caducifolio), often in disturbed or secondary forest. Habitats: shady canyons and ravines (barrancas). Phenology: flowering specimens have been collected January–February and June–July; mature fruiting material has been collected June–August and January.

Lycianthes michaelneei is a distinctive addition to series *Tricolores*. It is most commonly misidentified as *L. pilosissima* (M. Mart. & Gal.) Bitter (a synonym of *L. tricolor*), which is the name used for the species in the *Flora of Veracruz*. In using that name in *Flora of Veracruz*, Nee (1986) discussed its provisional nature. *Lycianthes michaelneei* differs from *L. tricolor* in having an entirely purple corolla (lobes and membrane) rather than a white membrane with some purple on the

Figure 2. Holotype of *Lycianthes michaelneei*.

lobes, a color pattern which is found in several species of series *Tricolores*. The label data for the type collection, which are quite detailed, does not mention the presence of green glandular spots on the corolla, and so I am assuming the spots are absent. In general, this species is more robust than other members of series *Tricolores*, with the longest leaves and leaf trichomes of any member of the series. Another distinctive difference is the matted stem hairs which are not found elsewhere in the series.

The specific epithet honors Michael Nee, Solanaceae expert and Curator Emeritus of the New York Botanical Garden who has mentored dozens of would-be Solanaceae taxonomists and annotated thousands of herbarium specimens wherever he has landed. His patience with me has been much appreciated. He collected the type specimen of *L. michaelneei* while employed at the Field Museum of Natural History, Chicago, working in conjunction with INIREB (Instituto Nacional de Investigaciones sobre Recursos Bióticos, now the Instituto de Ecología), Xalapa, on the *Flora de Veracruz* project.

Additional specimens examined. **MEXICO. Veracruz**. Mpio. Calcahualco, Barranca de Atotonilco, 2450 m, 14 Feb 1982, *Cházaro & Oliva 3293* (WIS); Mpio. Ayahualulco, parte alta Cerro Coatepec, a medio camino entre Ayahualulco y Patlanalan, 2600 m, 23 Aug 1985, *Cházaro & Acosta 3701* (WIS); Mpio. Calcahualco, 1 km al S de Escola, 19° 7' N, 97° 8' W, 1950 m, 24 Jul 1986, *Martinez 1227* (NY); Mpio. Calcahualco, San Miguel Tlacotiopa, camino a Nueva Vaqueria, Barranca Cuapa, 19° 6' N, 97° 14' W, 2600 m, 30 Jul 1985, *Martinez & Vásquez 525* (MEXU); Mpio. Calcahualco, 500 m al SW de Maquistla, camino a Jacal, 19° 7' N, 97° 11' W, 2200 m, 30 Jul 1985, *Martinez & Vásquez 538* (MEXU); Mpio. Acajete, Plan de Cedeño, 1750 m, 4 Jun 1981, *Ventura 18551* (IEB).

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OBSERVATIONS RELATIVE TO CLAIMS OF DISAPPEARANCE OF LILIACEAE AND ORCHIDACEAE IN CONCORD, MASSACHUSETTS, USA

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ABSTRACT

Historical evidence is reviewed in combination with field observations to evaluate the hypothesis that a disproportionate number of native species of Liliaceae and Orchidaceae have recently disappeared from Concord, Middlesex County, Massachusetts, and that this is attributable to climate change. The occurrence of the 16 native species of Liliaceae and 22 native species of Orchidaceae is reviewed. Only 3 of 16 Liliaceae species were formerly common and now possibly much less common or gone, while for Orchidaceae it is 6 of 22 species. Thus, the current study finds that evidence for any dramatic disappearance or decline in abundance in these families in Concord is weak. Further, a conclusion that only climate change has significantly affected the abundance of these 9 species is unwarranted, as many other causes in the Concord area are possible, e.g., reforestation, development associated with increasing population and suburbanization, degradation of water quality and air quality, predation associated with changes in animal populations, changes in land use, accidental burnings of woodlands, and spread of non-native plant species. In addition it is shown through historical examples, the author's observations, and comparison of floristic studies of the smaller Middlesex Fells Reservation, 10 miles distant from Concord, that determinations of what species are present in a local flora and of species abundances vary significantly.

In recent years dramatic claims have been made about mass extinction of native species in Concord, Massachusetts, particularly in certain families such as Liliaceae and Orchidaceae (Primack et al. 2009; Willis et al. 2008). The supposed disappearances have been attributed to climate change. This note reviews historical evidence and the varied experience of observers, present and past, to dispute those claims.

The most extensive floral explorations of Concord have been done by a long line of amateurs dating back to the early 19th century, even before the most prominent of these amateurs, Henry Thoreau (Eaton 1974). In the early 21st century a few professional botanists have undertaken surveys of parts of the town flora to evaluate a possible effect of climate change.

The following is a summary of historical sources for frequency of occurrence of plant species in Concord:

Henry David Thoreau (1817-1862). Thoreau studied the flora of the town most intensely from 1850 through 1860. Although he did not record frequency of occurrence for all the species he found, he wrote copious botanical observations about Concord plants and their localities in his Journal. In addition he collected a sizable, well-organized herbarium of pressed plants of approximately 1000 specimens, including many from his trips outside of Concord. Unfortunately, other than for the difficult groups of Poaceae and Cyperaceae, data other than identity is absent for most of these. While the frequency of occurrence for species in Concord can be estimated to some extent from the number of references in his Journal (using, for example, my botanical index to his Journal (Angelo 1984)), this is problematical without examination of the context of such references. For example, the rare *Lygodnum palmatum* (Climbing Fern) known then and now from only one locale in Concord is referred to approximately 20 times in his Journal, which is more than

the approximately 14 references in his Journal to *Comandra umbellata* (Bastard Toadflax), which Minot Pratt, Alfred Hosmer, and Richard Eaton all have agreed is common or very common.

Minot Pratt (1805-1878). Pratt was a Concord resident and friend of Thoreau, with whom he shared botanical information. Pratt lived in Concord from about 1845 until his death. He appears to have botanized throughout that time judging from references to him in Thoreau's Journal and the date of one of the only known herbarium specimens he collected in August 1872. He did not study all vascular plant groups in Concord as did Thoreau, but he did leave an impressive manuscript list of Concord plants (Pratt 1878) that includes most plant families with frequency of occurrence, habitat, and some specific locales for uncommon species. He did not maintain a herbarium, at least not one that has survived, so that the accuracy of his identifications cannot be assessed. However, some of his frequency information agrees with my personal experience more so than does Thoreau's, Hosmer's, or Eaton's for some distinctive species. Thus, it is likely he knew some parts of the flora better than his contemporaries and successors. Pratt is known to have introduced a number of species into Concord, mostly from Vermont and other parts of Massachusetts, and he noted most of them in his manuscript. None of the studies of species loss in Concord should include these introductions, as some have done, for example, in the preliminary list of missing Concord plants given to me by Primack and Miller-Rushing in 2007.

Alfred Winslow Hosmer (1851-1903). Hosmer was a life-long resident of Concord who apparently took up the study of botany about the time of Pratt's death in 1878 and pursued it primarily between 1888 and 1903, judging from the phenology data in his notebooks. Hosmer (like Pratt) did not study all plant families. Hosmer's notebooks (Hosmer 1903) extend to the year of his untimely death. Many more herbarium specimens collected by him survive than do Pratt's, but many fewer than Thoreau's and with little data other than identity and town of collection, typically Concord. Hosmer's manuscript notebooks provide flowering dates year-by-year (but unlike Thoreau, no record of locale for each date nor indication of whether at onset or peak or end of flowering), frequency of occurrence, and locales for some uncommon species. The problem with using Hosmer's notebooks for frequency of occurrence information is that they are not limited to Concord. The title of the notebooks says "Concord, Mass. and vicinity" and locales given for some species are in neighboring towns, such as Sudbury, Acton, and Lincoln. Frequency of occurrence is not necessarily the same for neighboring towns. For example, Thoreau, Pratt, and Eaton all agree that there was but one location in Concord for *Chamaecyparis thyoides* (Atlantic White Cedar). Yet Hosmer in his notebooks stated that this species was rather common. This discrepancy is understandable when one knows that extensive colonies of *Chamaecyparis* occur to this day in neighboring Sudbury and Bedford. Thus, use of Hosmer's frequency information must be approached with much caution when applying it strictly to Concord.

Richard Jefferson Eaton (1890-1976). Eaton was born and raised in Concord and botanized there from about 1920 until about 1970. He studied all vascular plant families. Through his long active membership in the New England Botanical Club, where he interacted with professional botanists, and through his 13 years as curator of the extensive NEBC vascular herbarium housed at Harvard University, he developed an expertise in plant identification that easily matched or surpassed all others who have studied or are studying Concord's flora, amateurs and professionals alike. His herbarium collections of Concord plants are the most extensive and contain the best information (habitat, locale, date of collection). Near the end of his life he published the most comprehensive account of the flora of the town to that date (Eaton 1974). His flora includes for each species: frequency of occurrence in Concord, habitat information, reference to a voucher specimen, and in some cases particular locales.

Recent studies of parts of the Concord flora and of another more limited area in eastern Massachusetts (Middlesex Fells Reservation) attempt to measure changes in species numbers in those floras. Two of these studies relate claimed changes in Concord to climate change:

(Drayton and Primack 1996). Drayton studied the flora of the Middlesex Fells Reservation, an area about 20% the size of Concord and located approximately 10 miles east of Concord. Drayton surveyed between 1990 and 1992, confining his study area to approximately 40% of the reservation and excluding ferns, graminoids, and aquatic plants. The findings, compared to results from an 1895 survey, resulted in a claim that 155 taxa were lost. Hamlin et al. (2012) noted that this paper has been cited widely for its conclusion that many taxa had been lost in the study area.

(Primack et al. 2009). In this study Primack and some of his students studied Concord's flora between 2003 and 2007. The study omitted about one third of the flora on the basis of difficulty in identifying the species in the field. It concluded that 27% of the species (native and introduced) seen by Thoreau could not be located and an additional 36% persist in only one or two populations where they are vulnerable to extinction. In addition, 20% of the 347 species seen by Edward Jarvis (1803-1889), as noted in his copy of Bigelow's (1824) "*Florula Bostoniensis*," are claimed as no longer occurring in Concord; 24% of 479 species seen by Hosmer similarly were no longer found; and 30% of 723 species seen by Eaton were no longer found in Concord. The study also asserted that in the past four decades (since Eaton's flora) that there has been a net loss of species (236 missing and 82 species gained). The authors assert that the losses appeared to be have been sustained mostly in the prior 30-40 years, with losses in certain groups, such as orchids, being particularly severe. The article noted that the manuscript of Pratt was not analyzed since his observations were claimed to overlap those of Thoreau and Hosmer. In fact, Pratt died only 16 years after Thoreau, and Hosmer's work concluded in 1903, 40 years after Thoreau's death, when changes in the Concord landscape due to reforestation were well underway.

(Willis et al. 2008). This study analyzed data for 473 Concord species (native and introduced) as noted by Thoreau, Hosmer, and Miller-Rushing, and Primack. Species were scored on such factors as changes in abundance, habitat, flowering time response to temperature (ability to track short-term seasonal temperature changes and shifts over long-term intervals), mean latitudinal range of the species, and native vs. introduced status. Among the results of the study was the observation that decrease in abundance was disproportionately high in certain families such as Asterales, Lentibulariaceae, Ranunculaceae (in part), Cornaceae, Liliaceales, Lamiaceae (in part), Orchidaceae, Saxifragaceales, and Malpighiales. The study further claimed that because the families particularly affected were the ones whose flowering times were not responsive to temperature change, that they were the ones whose abundance will be most affected by climate change.

(Hamlin et al. 2012). This work reported the results of a more intensive study of the entire Middlesex Fells Reservation over the period 2003 to 2011 by four principal investigators. In comparing the portion of the reservation studied by Drayton and Primack (1996), Hamlin et al. found 718 species of vascular plants (478 native), whereas Drayton and Primack found only 331 species (244) native, almost double the number of native species within the same study area. Equally striking was the comparison with the 1895 study of the reservation when the results of the Hamlin et al. (2012) study area were reduced to best fit the older study. Hamlin et al. found a total of 851 species (552 native, 299 introduced) while the 1895 study found a total of 680 species (570 native, 110 introduced). In summary, *there has been comparattvely little change tn the total number of natve species* (only 18 fewer species), while the number of introduced species nearly tripled (189 more species).

In the late 1970s and early 1980s I lived in and explored the flora of the town almost daily during the growing season and found a number of native plants thought to have disappeared (3 of 12 native species listed by Eaton (1974) as "Extirpated"). Much as Thoreau in *Walden* (1854, p. 20) with his lost hound, bay-horse and turtle-dove, I was still on the trail of the other so-called extirpated species at the time I left Concord. In 2007 I checked on a small sample of species, determined by my physical ability to reach stations where I had seen them, claimed to be missing by Richard Primack of Boston University and his student, Abraham Miller-Rushing, who were studying the Concord flora. All but one of those species that I was able to revisit were still where they had been and in about the same abundance. These were not the only stations in town where I had seen them and not the stations with the most plentiful quantities (that I could no longer reach). Primack (pers. comm.) dismissed my findings of the continued presence of the given species, noting mainly that there were too few plants and thus they were practically extinct, as if these were the sole locales for the species in Concord. However, I found no compelling evidence for mass disappearance in Concord in the previous 30 years, contrary to the conclusion of Primack and his students (Primack et al. 2009).

I have intimate familiarity with the records of the key amateur botanists of Concord's past who left written information on their finds (Thoreau, Pratt, Hosmer, Eaton), and in late 2012 I set about compiling a detailed online flora of Concord that would summarize and compare their observations with my own from my notes and from my herbarium vouchers (see Angelo 2014). In the course of that work I noticed that the native Liliaceae and Orchidaceae of Concord are not disproportionately disappearing, even accepting for the sake of argument that particular species may no longer be present. As these two families are among those claimed to be experiencing loss of species, I did some simple counting to check on my sense of this.

The historical record (Angelo 2014) shows that 16 native species of Liliaceae *sensu lato* have been found in Concord (nomenclature for the two families is from Angelo and Boufford 2000):

**Allium canadense* var. *canadense* (Wild Garlic)
Clintonia borealis (Yellow Clintonia)
Hypoxis hirsuta (Common Stargrass)
Lilium canadense (Canada Lily)
Lilium philadelphicum (Wood Lily)
Maianthemum canadense (Canada Mayflower)
Maianthemum racemosum subsp. *racemosum* (False Solomon's-seal)
**Maianthemum stellatum* (Star-flowered False Solomon's-seal)
**Maianthemum trifolium* (Three-leaved False Solomon's-seal
Medeola virginiana (Indian Cucumber-root)
Polygonatum pubescens (Small Solomon's-seal)
Trillium cernuum (Nodding Trillium)
**Trillium undulatum* (Painted Trillium)
**Uvularia perfoliata* (Perfoliate Bellwort)
Uvularia sessilifolia (Wild-oats)
Veratrum viride (White Hellebore)

Five species in the list above (with asterisk) were rare or merely occasional in Thoreau's time, and the inability to relocate them now would not be a fair measure of disappearance. The list is thus reduced to only 11 species, a very small sample size. The following are still common and relatively easy to find: *Hypoxis hirsuta*, *Maianthemum canadense*, *Maianthemum racemosum* subsp. *racemosum*, *Medeola virginiana*, *Polygonatum pubescens*, *and Uvularia sessilifolia* (personal observation and Cherrie Corey, pers. comm. 2014). However, I did find *Clintonia borealis* and *Veratrum viride* in my physically limited visits in 2007, so that these are not truly gone and most likely occur at other Concord sites that I could not revisit. This is confirmed for *Veratrum* by Cherrie Corey,

a Concord resident and naturalist, who reports *"Veratrum* grows abundantly and with vigor throughout many of the wet seeps in Estabrook Woods … Last year I saw it somewhere else too," (pers. comm. 2014). Eaton (1974), who most extensively documented the flora of Concord, recorded *Veratrum* as common and *Clintonia* as frequent. This accords with my experience in the 1970s and 1980s. Thus, 7 of the 11 species are still common, and, if in fact *Clintonia* has significantly declined in frequency, it is a very precipitous decline within the period of only 20 years, unlikely due to climate change. This is because the northeastern USA increase in mean temperature per decade after 1970 was 0.5 degrees Fahrenheit (Northeast Climate Impacts Assessment 2007), while the geographical range of *Clintonia borealis* is from northern Georgia to Labrador, where a significantly greater difference in mean temperatures occurs. Far greater temperature fluctuations also occur in Concord year-to-year.

This leaves possibly 3 species formerly common that are either gone or much less common, *Lilium canadense*, *Lilium philadelphicum*, and *Trillium cernuum*. I was unable to verify the recent status of these three species, all of which I saw when I lived in Concord. Eaton stated in 1974 that *Lilium canadense* was common, *Lilium philadelphicum* was frequent but scarce, and *Trillium cernuum* was uncommon, which accords with my experience in the 1970s and 1980s except that I found *Lilium philadelphicum* to be occasional, and scarce where it did occur. *Lilium philadelphicum* requires dry, open habitats, habitats which have been vanishing in Concord. Hamlin et al (2012) also reported that *Lilium* populations are under strong impacts from herbivory by Scarlet Lily Beetles and White-tailed Deer, which could account for a reduction in their populations.

If in fact these 3 Liliaceae have disappeared, it has happened mostly in the period of 20 years which would suggest reasons other than climate change for the reasons noted above. The disappearance claim for Liliaceae disappearing in Concord thus revolves around the uncertain status of only 3 out of 11 native species that were common in Thoreau's time, which is an insignificant sample size to draw conclusions, and the likelihood of causes other than climate change is significant.

The historical record (Angelo 2014) shows that 22 species of native Orchidaceae have been found in Concord:

Arethusa bulbosa (Arethusa)
Calopogon pulchellus (Grass-pink)
**Corallorhiza maculata* (Spotted Coral-root)
Cypripedium acaule (Pink Lady's-slipper)
Goodyera pubescens (Downy Rattlesnake-plantain)
**Goodyera* x *tesselata* (Checkered Rattlesnake-plantain)
**Isotria verticillata* (Large Whorled Pogonia)
**Liparis lilifolia* (Large Twayblade)
**Liparis loeselii* (Loesel's Twayblade)
**Platanthera blephariglottis* var. *blephariglottis* (White Fringed Orchis)
Platanthera clavellata (Green Woodland Orchis)
**Platanthera dilatata* var. *dilatata* (Bog Candle)
**Platanthera flava* var. *herbiola* (Tubercled Orchis)
**Platanthera grandiflora* (Large Purple Fringed Orchis)
Platanthera lacera (Ragged Orchis)
**Platanthera orbiculata* var. *macrophylla* (Large Round-leaved Orchis)
Platanthera psycodes (Small Purple Fringed Orchis)
Pogonia ophioglossoides (Rose Pogonia)
Spiranthes cernua (Nodding Ladies'-tresses)
Spiranthes lacera var. *lacera* (Northern Slender Ladies'-tresses)
Spiranthes lacera var. *gracilis* (Northern Slender Ladies'-tresses)
**Spiranthes ochroleuca* (Yellow Ladies'-tresses)

Again, to meaningfully assess disappearance since Thoreau's time those species rare or occasional in his time should be recognized (with asterisk). This leaves 11 species formerly more or less common, a small sample size. Of these 11, *Cypripedum acaule* and *Goodyera pubescens*, both dryland species, are still common or frequent and easy to find (Cherrie Corey, pers. comm. 2014). Of the remaining 9, I observed in Concord in the early 1980s *Platanthera psycodes*, *Pogonia ophioglossoides*, and *Spiranthes cermua* but only at very few locations. Eaton (1974) noted *Platanthera lacera*, *Spiranthes cernua*, and *Spiranthes lacera* var. *lacera* as still common or frequent. Thus, of the 11 native species formerly common in Concord at least 5 were still common in 1974. Of the remaining 6 species, 3 (*Arethusa bulbosa*, *Platanthera psycodes*, and *Pogonia ophioglossoides*) were particularly common in Thoreau's time in river meadows that became seriously polluted in Concord in the 1930s according to Eaton (1974), resulting in significant changes to the river meadow flora after that time. Two others (*Calopogon pulchellus* and *Platanthera clavellata*) of the remaining 6 are primarily found in bogs and swamps where their decline might also be associated with water quality issues since Thoreau's time. In summary, while there is perhaps a better case for disappearance of native Orchidaceae formerly common in Concord than for Liliaceae, the sample size is small and the likelihood of causes other than climate change is significant.

Determining the presence, absence or frequency of occurrence of a given species in a sizable tract of land at a given time is not an easy or simple task. My study of what the historic Concord botanists were able to find or failed to find in Concord after their years of careful exploration reveals surprising differences from species to species. One of the most dramatic differences is for the relatively easily recognized fern, *Phegopteris connectilis* (Long Beech Fern). Pratt (1878) said that it was common, while Thoreau did not mention this species at all in his Journal and had no specimen of it in his herbarium. Hosmer (1903) noted its occurrence at only one swamp in Concord, while Eaton (1974) included it in his list of rare species for which the current status was unknown. Yet, in the late 1970s and early 1980s I found this fern plentiful in at least six localities that were clearly natural for this species.

This raises the issue of the ability of field biologists to find plants. Experienced botanists know that some people are more skillful at this than others. The ability depends on acuity and experience as well as on the search intensity and on being at the right place at the right time. A large, very showy population of *Castilleja coccinea* (Painted Cup) escaped the notice of the keen-eyed Thoreau until he happened upon it on May 8, 1853, at age nearly 36, prompting him to remark in his Journal that "It is wonderful what a variety of flowers may grow within the range of a walk, and how long some very conspicuous ones may escape the most diligent walker, if you do not chance to visit their localities in the right week or fortnight, when their signs are out." A more quantifiable, recent example of the variation among different investigators, arriving at significantly different results for plants in a given area is the case of the flora of the Middlesex Fells Reservation, as noted above. This flora was studied in 1993 leading Drayton and Primack (1996) to claim that 155 plant taxa had been lost. Yet Hamlin and his co-authors (Hamlin et al. 2012) who searched the same area of the Middlesex Fells Reservation over a longer period found that 105 (68%) of those putatively "lost" species were not missing. Equally important is that in the 15 month period following the impressive 2012 study, *new native species and additional locations for rare or uncommon species continue to be found* in the Middlesex Fells Reservation. Hamlin and Kittredge (2013) reported that 22 new plant taxa were found, of which 9 are native, and that new locations for 67 less common taxa were found. Different results will ensue depending on the investigator and intensity of investigation. Based upon all that has been pointed out above it is a contention of this article that no person or small group of persons can accurately measure in a limited span of time the entire extent of a flora the size of a town such as Concord or even of a much smaller area such as the Middlesex Fells Reservation, where such a diversity of habitats exists.

Finally, as noted in more detail in the introduction of my online Concord Flora, changes undoubtedly have occurred in the flora and vegetation of Concord since Thoreau's time, since it is part of a huge, extremely complex, integrated, dynamic ecological system constantly evolving in time. Enormous changes have clearly occurred in the landscape of Concord from Thoreau's time to the present, including areas currently under protection, due primarily to reforestation (a regional phenomenon), development associated with increasing population and suburbanization, and spread of non-native plant species. Key botanical hot spots have been ruined since Thoreau's time by construction or landowner "improvements" (e.g., Clamshell Hill by Route 2, a four-lane highway, and the fabulous *Ledum* Swamp by drainage and cutting by a succession of owners). In addition there surely are a myriad of other changes that are less visually apparent — degradation of water quality and air quality, predation associated with changes in animal populations (not just deer, but both vertebrate and invertebrate and microbial), disappearance of pollinators, changes in land use (such as, using woodlands for firewood, decline of and change in types of farming), radiation changes associated with changes in the atmosphere, climate change, significant accidental burnings of woodlands (such as the one of more than 300 acres beside Fairhaven Bay caused by Thoreau and Edward Hoar in 1844, for which many townsfolk remembered Thoreau for decades rather for than any of his writings, and the one in Walden Woods in the 1930s that destroyed one of the last, or the very last, colony of *Linnaea borealis* (Twinflower) in Concord according to Eaton (1974)), and factors not even thought of. Simply documenting and measuring changes in native plant populations in Concord is problematic in itself, but assigning a cause or causes to purported changes would require multidisciplinary studies of the numerous complex ecological processes at play in order to determine their effects on plant population dynamics.

The world's climate undoubtedly is changing, and the local climate of Concord is changing with it, indicated by earlier flowering and leaf-out times in the area (Ellwood et al. 2013). The study by Willis et al. (2008), however, does not appear to document the effect of climate change on the Concord flora. Their conclusion is directly predicated on the premise that species presence and abundance in certain plant groups is significantly declining, which is challenged here for Liliaceae and Orchidaceae, two of the groups for which they found decline but for which better sampling shows the continued presence and abundance of the species. The assumption, essential for the recent mass disappearance studies of Concord, that it is possible to gauge with sufficient accuracy the degree of presence of particular vascular plants species at certain points in time, is seriously questioned by a review of historical records of the most experienced Concord botanists.

"Absence of evidence is *not* evidence of absence." -- Carl Sagan (1997, p. 213).

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LECTOTYPIFICATION OF *CONVOLVULUS WHELERI* (CONVOLVULACEAE)

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ABSTRACT

Although a specimen at the Natural History Museum of Denmark (C) is labeled as the holotype of *Convolvulus wheleri* Vahl, that is an error. This name was based on an uncited specimen from Spain and Vahl listed Plukenet's polynomial *Convolvulus Sagittariae foliis, flore purpureo, Wheleri* in synonymy. Because there is a specimen for the Plukenet name, the Vahl binomial is based on syntypes. Both specimens are discussed and the sheet at C, collected in 1762 at Lago La Albufera, Valencia, Spain, by *Barnades*, is selected as lectotype of *Convolvulus wheleri*.

When Vahl (1791, p. 36) proposed the name *Convolvulus wheleri,* he cited no specimen but wrote that the plants were "*In Hispanum juxta lacum la Albufeda Valentiae.*" McDonald (1994, p. 106) listed a specimen in the Vahl herbarium at Copenhagen labeled "*Ex incultis juxta lacum La Albufeda Valentiae*" as the holotype in *Flora de Veracruz*, based on the assumption that this was the only original material for *C. wheleri* available (Fig. 1). In calling the specimen a holotype, McDonald, like many others, was unaware of a Wheler collection at BM that was annotated with the phrase name "*Convolvulus Sagittariae foliis, flore purpureo, Wheleri"* by Plukenet (1691, p. 113, tab. 85. f. 3), a name cited in synonymy by Vahl. That particular specimen was noted by Britten (1894, p. 170) who recognized it as the "type" of the Plukenet polynomial. Moreover, Britten said that the specimen was in the Sloane herbarium (BM) in the Hort. Sicc. Vol. 91, fol. 57 (Fig. 2).

While the first author was working on a study of the introduction of *Ipomoea sagittata* Poir. into the Mediterranean (Austin, in press), he discovered the Britten comment and realized that the Vahl sheet was not a holotype. Consequently, the Vahl name is clearly based on syntypes. In spite of the fact that *C. wheleri* is an illegitimate, superfluous name for *Ipomoea sagittata* Poir. and now widely cited in synonymy, a lectotype needs to be selected from the syntypes. We do that here.

Ipomoea sagittata Poir., Voyage en Barbarie 2: 122. 1789. **TYPE: ALGERIA.** Nous avons trouvé cette plante avec M. Desfontaines, près du Bastion de France & sur les bords du lac infect qui en est peu distant, dans le voisinage du Souk [from protologue], *Desfontaines* s.n. (holotype: P).

Convolvulus wheleri Vahl, Symbolae Botanicae 2: 36. 1791, nom. illeg. superfl. **LECTOTYPE** (designated here): **SPAIN. VALENCIA.** Ex incultis juxt. Lacum La Albufera, 1762/8, *Dr.* [*Miguel*] *Barnades s.n.* (C, barcode no. C10009688!). Syntype as cited below.

Figure 1. Lectotype of *Convolvulus wheleri* Vahl collected in Valencia by *Barnades*. On the back of sheet is written "August 1762. Ex incultis juxt. Lacum La Albufera Valentiæ." With permission of the Natural History Museum of Denmark (C).

Figure 2. Syntype of *Convolvulus wheleri* Vahl collected by Sir George Wheler in Zante [Ζάκυνθος], 24 to 28 July 1675. Annotated by Leonard Plukenet with *Convolvulus Sagittariae folius, flore purpureo, Wheleri, in Inventore habui*. Sir Hans Sloane added the "R. H. 1882." The pencil notes were written by James Dandy. With permission of the Natural History Museum (BM).

Syntype of *Convolvulus wheleri* Vahl. **GREECE.** [Zante, 24–28 Jun 1675, *George*] *Wheler s.n.* (BM). *Convolvulus Sagittariae folits, flore purpureo, Wheleri ab Invetore habui* Plukenet, Phytographia, tab. 85, f. 3. 1691. *Convolvulus vulgaris major, flore amplo, dilute purpureo* Plukenet, Almagestum botanicum, 113. 1696.

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Ib Friss (C) and Ole Seberg (C), Charley Jarvis (BM), and Mark Carine (BM) provided information and photographs of critical specimens. Jarvis identified the handwriting on the Wheler specimen.

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DISCOVERY OF *SOLIDAGO PORTERI* (ASTERACEAE: ASTEREAE) IN ALABAMA AND TENNESSEE AND A SECOND POPULATION IN GEORGIA

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ABSTRACT

Solidago porteri Small was thought to be known only from the type collection from Monticello in Jasper Co., Georgia, in the southeastern U.S.A. In 2003, a collection that is now recognized to be the same species was made in Hartselle in Morgan Co., Alabama. In 2004, a collection that is also now recognized to be the same species was made in Giles Co., Tennessee. Exchange of information between the authors resulted in additional material being collected at the Tennessee site in 2012. A review of photographs of types at NY revealed that the Alabama and Tennessee collections were recent collections matching the type material of *S. porteri*. Both the Alabama and Tennessee collections were determined to be hexaploid $2n = 27_{II}$. A search for additional collections in the GA herbarium in 2014 yielded a set of *S. porteri* plants from Morgan Co., Georgia. Details of the morphology and distribution are discussed.

Solidago porteri Small was described in 1903 from a T.C. Porter collection made in Monticello (Jasper Co.), Georgia, in 1846. Figure 1 shows a previously unrecognized isotype, *Porter s.n.* (NY; Thiers 2014). Guy Nesom annotated the specimen as *S. buckleyi* Torr. & A. Gray in 1990 (see Semple and Gandhi 2012), and J.C.S. included the specimen in an unpublished multivariate study of *S.* subsect. *Thyrsiflorae*, before its correct identity was known. The attached note on the specimen indicates that A. Gray and Canby also had trouble with identifying the collection in the 1800s. Cronquist (1980, p.122) included the following statement about *S. porteri* under *S. hispida* Muhl.: "Known only from [holotype] type collection, suggests a robust form of *S. hispida*, but less hairy (stem glabrous below, rather sparsely spreading-hirsute above) and has a somewhat wider and looser inflorescence. The proper disposition of this name is uncertain." Semple and Cook (2006) in Flora North America treated the species as a synonym of *S. erecta* Pursh, based on the type having similar variation in stem hair distribution as well as typical subsect. *Squarrosae* traits of large lower stem leaves and a club/wand shaped arrangement of heads.

In 2003, a single individual was collected along a roadside just south of Hartselle, Alabama. Three shoots were pressed (*Semple & Semple 11190* WAT; Fig. 2) and involucre buds were fixed for later chromosome counting from meiotic figures. No photographs were taken in the field and the plant was labeled *Solidago petiolaris* Ait. var. *petiolaris* because the plant was nearly a meter tall and had multiple stems developing from the rootstock. Traits of the specimen were scored for a multivariate study of *Solidago* subsect. *Thyrsiflorae* A. Gray, but J.C.S. later realized that the

collection did not possess the traits of that subsection. It was subsequently erroneously labeled *S. patula* Muhl. subsp. *patula*. The collection came from the area between the known distributions of *S. patula* and *S. salicina* Ell. (synonym: *S. patula* ssp. *strictula* (Torr. & A. Gray) Semple; see Semple et al. 2012), although the hexploid chromosome count (see below) for *Semple & Semple 11190* was unknown for either of these species of *Solidago* subsect. *Argutae* (Mackenzie in Small) Nesom. The correct identity of the collection as *S. porteri* was not determined until September of 2012 following additional field and herbarium work.

In 2004, a population of what was initially thought to be *Solidago petiolaris* was discovered in Giles Co., Tennessee: *Estes 6795* APSC. Cypselae were taken and planted by D.E in his home garden. Email was exchanged between the authors in 2006 regarding the identification of this collection. When J.C.S. decided in the summer of 2012 that his Alabama collection was possibly a new species in *Solidago* subsect. *Squarrosae* A. Gray, email was again exchanged and field work was planned so that both authors could see the Tennessee population and determine if it was conspecific with the Alabama population, which it was.

On 12 Sep 2012, the Tennessee site was sampled again (*Semple, Estes, Campbell, & Brock 11861* BRIT, GA, DAO, GH, MO, NY, TENN, and WAT, 3 sheets) and then on 13 Sep 2012 (*Semple 11867* MO, NCU, WAT, US), when light conditions were more conducive for taking habitat photographs. The large sample was taken to obtain sufficient specimens for inclusion of the taxon in a multivariate morphometric study of *Solidago* subsect. *Squarrosae* being carried out in the J.C.S. laboratory. Efforts to find other populations in adjacent Lawrence Co. near the Giles Co. population were unsuccessful.

The 2003 Alabama site was also visited on 13 Sep 2012 but was not relocated. In 2003, US-31 was a two-lane road and the plant was growing on the road embankment. In 2012, US-31 was a four-lane road and no plants of *S. porteri* were seen. Highway construction apparently extirpated the only currently known location of the species in Alabama. A search along other roads in and around Hartselle failed to turn up another population of the species.

The University of Georgia herbarium (GA) was visited on 17 March 2014 and a search of *Solidago* collections was made to find additional specimens of *S. porteri*. No specimens were filed under the name *S. porteri*. Folders of *S. bicolor*, *S. erecta*, *S. hispida*, and *S. petiolaris* were examined but did not include specimens of *S. porteri*. A folder labeled "Solidago hybrid swarm" was examined and this contained four specimens of *S. porteri* from north of Rutledge, Morgan Co., Georgia: *J.W. Hill 1162a* (GA); *J.W. Hill 1162b-1* (GA; two sheets; Fig. 3); and *J.W. Hill 1162c-6* (GA). These came from "open pine woods," "mature hardwoods," and "open sunny near lake [Lake Rutledge]" on 6 September 1979. Morgan County is just north of the type locale in Jasper Co., Georgia. Heads of these specimens were in bud stage to mature fruiting stage. The Hill collections indicate that the species had survived in this part of the Georgia Piedmont for 137 years. The lack of other recognized collections of *S. porteri* from the area or elsewhere in Georgia is probably indicative of the rarity of the species. In Alabama the species is known from only one site, where now extirpated. In Tennessee the species is known from a single population consisting of fewer than 50 individuals.

Physiography

Both the Alabama and Tennessee populations of *Solidago porteri* are/were situated within the Interior Low Plateaus Physiographic (ILP) Province. The Tennessee site (Figs. 4-6) is in the Western Highland Rim Subsection, Highland Rim Section of the ILP. This area is primarily underlain by Mississippian-aged cherty limestone of the Fort Payne formation. Historically, this area was dominated by a mix of native grassland and oak savanna, areas often referred to as barrens. These

barrens, which were restricted mostly to the broad, flat uplands are common to portions of western-most Giles Co., much of adjacent Lawrence Co., extreme southwestern Maury Co., and parts of southeastern Lewis Co. Today, remnants of this once extensive barrens vegetation are found mostly along roadsides and include typical species such as *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Helianthus eggertii*, *H. silphioides*, *Tephrosia virginiana*, numerous species of *Lespedeza*, *Desmodium*, and *Liatris spicata*. Much of this region has succeeded into oak-hickory woodland and the presence of scrubby post oaks and blackjack oaks, the typical oaks of the barrens, is a further indication of the once former grassland/savanna physiognomy. A large amount of the wooded landscape has been timbered at least a couple of times and much of it has been converted to loblolly pine (*Pinus taeda*) plantations, a species which is native only a few miles to the south in northern Alabama. Clearcuts are abundant in the area and many of the clearcuts contain numerous barrens species soon after harvest. Much of the area not in woodland has been extensively cultivated in cotton and soybeans.

In addition to *Solidago porteri*, other rare barrens species found in southwestern Giles Co., Tennessee, include *Bradburia pilosa* and *Helianthus eggertii*. For the *Bradburia*, this is the only region of Tennessee where it is known to occur. *Helianthus eggertii* is endemic to the Highland Rim barrens of the Interior Low Plateau of south central Kentucky, Tennessee, and northern Alabama. The barrens are mostly dry, but wet barrens undoubtedly once were more extensive in the region as well. *Solidago porteri* grows in dry soil at the margin of a ca. 10-year old clearcut that has been planted in loblolly pine monoculture. The pines are so dense and have grown so much since the discovery of *Solidago porteri* in 2004 that the goldenrod is actually in danger of being shaded out at this locality.

The Alabama site is also located in the ILP but is 75 km south-southeast of the Tennessee, population. It occurs very near the border of the Little Mountain portion of the ILP and the Moulton Valley, which is considered a lobe of the Eastern Highland Rim Subsection, Highland Rim Section of the ILP. The Little Mountains are a small, east-west trending ridge system that extends for ca. 112 km of northwestern Alabama across portions of Colbert, Franklin, Lawrence, and Morgan counties. The geology of the LM is primarily Mississippian sandstone, underlain by Mississippian limestone. Most of this ecoregion is currently wooded or in pasture. The Moulton Valley parallels the Little Mountains to the south and is sandwiched between the Little Mountains and the Cumberland Plateau. This limestone valley, of Mississippian age, is mostly flat and is characterized by many limestone cedar glades.

Moulton Valley supports a wide range of species, including those with calcareous and acidic preferences, dry prairie and glade species, and wetland species. The collections from Hartselle were collected in an oak savanna, a habitat that is quite similar in some respects to the Tennessee site, which would have historically been oak savanna or oak barrens, as they are often called. The Moulton Valley is known for containing a number of endemic plant species. The limestone glades there support a number of rare and restricted species, including several not known to occur outside of the Valley. These include *Leavenworthia crassa*, *L. alabamica*, *and Sisyrinchium calciphilum*.

A few rare plant species make similar range disjunctions between southwestern Middle Tennessee barrens and similar habitats in northwestern and north-central Alabama. *Helianthus eggertii* and *Silphium mohrii* both are endemic or nearly so to Highland Rim grasslands and occur in these two major regions. A new and highly restricted species of *Lysimachia*, under study by D. Estes, also makes a similar jump. Ninety-five percent of this taxon's worldwide range is restricted to the dry-xeric oak woodlands of eastern Lewis Co. and extreme southwestern Maury Co, Tennessee. From these populations the species jumps southward to the oak woodlands in Blount Co., Alabama, in the southern Cumberland Plateau. *Solidago porteri* makes a similar jump from south-central

Tennessee to north Alabama region and additionally jumps to the Georgia Piedmont, with its type locality located near Monticello in Jasper Co., and the 1979 collections from Morgan Co., Georgia.

While the odd distribution of *Solidago porteri* raises phytogeographic questions, other species have somewhat similar patterns of disjunction. The rare whorled sunflower, *Helianthus verticillatus*, is found in two localities in the Coastal Plain of southwest Tennessee and is disjunct to the Coosa Valley of northeastern Alabama and northwestern Georgia and is known from nowhere else. Likewise, *Silphium mohrii* is found discontinuously in a crescent-shaped arc extending from south-central Tennessee through northern Alabama to northwestern Georgia's Ridge and Valley and Cumberland Plateau provinces.

Morphological comparisons

Solidago porteri is a member of *Solidago* subsect. *Squarrosae* with similiarities to *S. hispida* but has noticeably larger heads with more showy rays. Collections from the four known populations sampled were initially identified as members of subsect. *Thyrsiflorae*, either as *S. buckleyi* (Fig. 1) or *S. petiolaris* (Fig 2A) or as samples of a hybrid swarm without parents designated (Fig 3A). The robust size of the some plants with multiple stems and the sometimes large lower and mid stem leaves with serrations (Figs. 1C,E and 2A) are traits of *S. buckleyi* and sometimes *S. petiolaris*. The inflorescence (Figs. 2A, 3A and 4E) can be similar in appearance to that of plants of *S. arenicola* Keener & Kral, which is native to northern Alabama and northern Tennessee and adjacent Kentucky and is a member of *Solidago* subsect. *Humiles* (Rydb.) Semple. This is likely convergence due to the larger involucres (Fig. 5) of the two polyploid species. No resin or glands typical of species of subsect. *Humiles* were observed on any of the collections of *S. porteri*. The largest leaves are basal (Fig. 3A), which is typical of subsect. *Squarrosae*, but not subsect. *Thyrsiflorae*. Rosettes were observed at the Giles Co., Tennessee, site in 2012 but were rare. These did not appear to be produced from lateral branches of rootstocks that bore flowering stems, which is a common growth form in subsect. *Squarrosae*.

Preliminary results of the unpublished multivariate study by J.C.S. and his students are significant. A stepwise discriminant analysis was used to generate a discriminant function for placing specimens a posteriori into the a priori species level groups using a combination of leaf and floral traits. All eight specimens of *Solidago porteri* were placed into *S. porteri* and seven of these were placed in *S. porteri* with 97-100% probability. The only other species whose specimens were placed as strongly a posteriori into its priori group was the very distinctive *S. villosicarpa* LeBlond. In the plot of canonical variate scores, *S. porteri*, *S. villosicarpa*, and *S. squarrosa* Muhl. were separated on the first and second axes from all other species in the subsection. Additional work is needed to complete the multivariate study. Preliminary results indicated that *S. porteri* is a morphologically very distinct species in spite of the fact that is has been misidentified or placed in synonymy by nearly everyone, including the authors, until now.

Chromosome numbers and cytological observations

The following two chromosome counts by J.C.S. were determined from pollen mother cells undergoing meiosis. The methods were those described in Semple & Cook (2004). In addition, anther sacs of *Semple et al. 11861* (same population as *Estes 06795*) were examined from head buds fixed in the field, but these turned out to be male sterile. No pollen mother cells or mature pollen were observed in multiple floret buds dissected.

Solidago porteri Small. $2n = 27_{II}$. **USA. Alabama**. Morgan Co.: US-31 S end of Hartselle, 4.7 km S of US-36, oak savannah in area with houses, 5 Sep 2003, *J. Semple & B. Semple 11190* (WAT).

Solidago porteri Small. $2n = 27_{II}$. **USA. Tennessee**. Giles Co.: ca. 4 mi NW of Minor Hill (SW of Paulaski), W side of Little Texas Rd., S of intersection with Kennedy Rd., barren roadside, 30-40 plants present, 21 Aug 2004, *Estes 06795* (APSC; from F1 plant grown in Clarkesville, TN).

Description in Flora North America style (mean values in **bold**)

Plants 34–**67**–104 cm; caudices short branched. **Stems** usually single to 6, glabrous proximally, sparsely to moderately strigose in inflorescence. **Leaves**: proximal most withering, smaller; basal and proximal cauline tapering to winged petioles, blades elliptic to elliptic-obovate or oblanceolate, mostly 46–**94**–150 × 14–**23**–53 mm, margins serrate, 1–7–17 serrations per side, usually acuminate, glabrate or sparsely strigose on the adaxial surface, sparsely to moderately strigose on the veins and abaxial surface; mid and distal cauline sessile, blades mostly rhombic-elliptic to narrowly lanceolate, mid cauline 38–**65**–153 × 9–**16.5**–38 mm, upper cauline 20–**35**–65 × 6–**9.7**–18 mm; margins becoming less serrate on more distal leaves. **Heads** 5–75, in elongate, narrowly paniculiform arrays, 30–220 mm long, leafy-bracteate proximally, not secund, proximal branches sometimes elongated and ascending. **Peduncles** 1–6 mm, bracteolate. **Involucres** cylindrical-campanulate, 6–**7.2**–9.5 mm. **Phyllaries** in 3–4 series, appressed, unequal (outer 1/4 length of inner), linear-oblong to lanceolate, apices obtuse to rounded. **Ray florets** 4–**6**.5–8; laminae 2–**3.2**–4.5 × 0.8–**1.4**–2.1 mm. **Disc florets** mostly 9–**11**–15; corollas 3.5–**5.1**–6.2 mm, lobes 1.1–1.9–2.1 mm. **Cypselae** (tan) 1.75–3.5 mm, usually glabrous, sometimes sparsely strigose; **pappi** 3.6–5.8 mm. **2*n*** = 54.

Additional specimens of *S. porteri* are likely hidden away in other herbaria under various names other than *S. porteri*. The multiple images and detailed description included here are provided to aid others in finding these specimens.

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Figure 1. A previously unrecognized isotype of *Solidago porteri* Small, *Porter s.n.* (NY).

Figure 2 *Solidago porteri* morphology, Alabama (*Semple & Semple 11190*, WAT) **A.** Shoot **B.** Lower stem **C.** Lower stem leaf detail, adaxial surface **D.** Mid stem detail **E.** Mid stem leaf, abaxial surface **F.** Ray and disc florets and disc floret corolla (immature). Scale bar = 1 mm in B, D-F; = 1 cm in C.

Figure 3 *Solidago porteri* morphology, Georgia. **A.** Shoot (*J W Hill 1162b-1,* GA, sheet 1) **B.** Upper stem and leaf surfaces (*J W Hill 1162b-1,* GA, sheet 2) **C.** Fruiting heads (*J W Hill 1162a,* GA) **D.** Disc floret cypsela (*J W Hill 1162a,* GA). Scale bar = 1 mm in B, D, = 1 cm in C

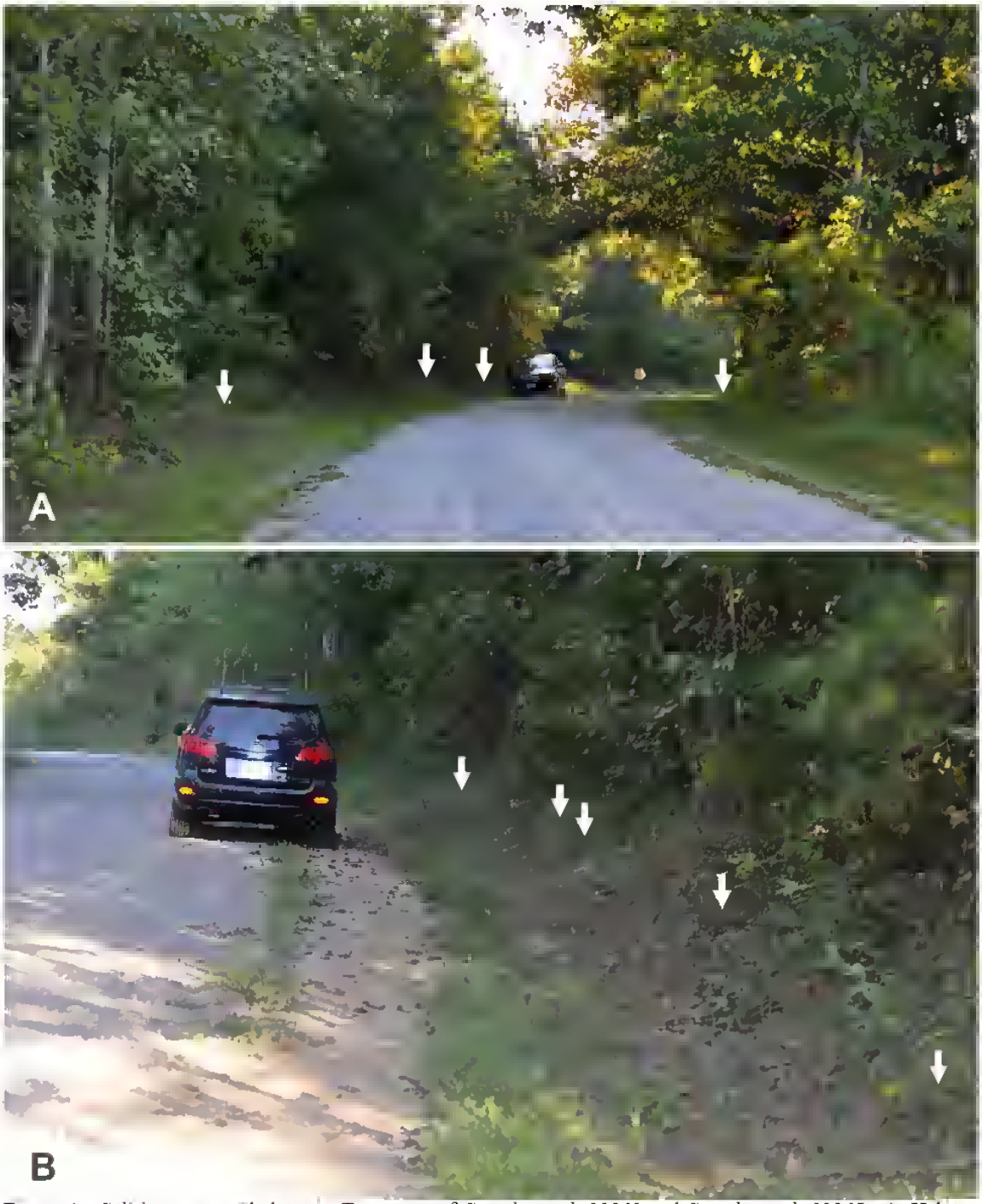

Figure 4. *Solidago porteri* habitat in Tennessee of *Semple et al. 11861* and *Semple et al. 11867*. **A.** Habitat looking north **B.** Habitat looking south along west side of road. Locations of plants indicated by arrows

Figure 5 *Solidago porteri* morphology, Tennessee (*Semple et al. 11861*) **A.** Shoots **B.** Mid stem leaves **C.** Mid stem detail **D.** Mid stem leaf detail, abaxial surface **E.** Inflorescence

Figure 6. *Solidago porteri* floral morphology, Tennessee *(Semple et al. 11861)*. **A.** Part of an inflorescence. **B.** Heads showing involucres. **C.** Head showing rays, most disc florets not yet open.

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CITRUS TRIFOLIATA (RUTACEAE): REVIEW OF BIOLOGY AND DISTRIBUTION IN THE USA

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ABSTRACT

Citrus trifoliata (aka *Poncirus trifoliata*, trifoliate orange) has become an aggressive colonizer in the southeastern USA, spreading from plantings as a horticultural novelty and use as a hedge. Its currently known naturalized distribution apparently has resulted from many independent introductions from widely dispersed plantings. Seed set is primarily apomictic and the plants are successful in a variety of habitats, in ruderal habits and disturbed communities as well as in intact natural communities from closed canopy bottomlands to open, upland woods. Trifoliate orange is native to southeastern China and Korea. It was introduced into the USA in the early 1800's but apparently was not widely planted until the late 1800's and early 1900's and was not documented as naturalizing until about 1910.

Citrus trifoliata L. (trifoliate orange, hardy orange, Chinese bitter orange, mock orange, winter hardy bitter lemon, Japanese bitter lemon) is a deciduous shrub or small tree relatively common in the southeastern USA. The species is native to eastern Asia and has become naturalized in the USA in many habitats, including ruderal sites as well as intact natural commmunities. It has often been grown as a dense hedge and as a horticultural curiosity because of its green stems and stout green thorns (stipular spines), large, white, fragrant flowers, and often prolific production of persistent, golf-ball sized orange fruits that mature in September and October. The fruit peels are sometimes used for marmalade, but the fruits are intensely sour or bitter. "Don Shadow, a nurseryman in Tennessee, has a recipe for poncirus-ade: Take a barrel of water, a barrel of sugar, and add one sour fruit (Klingaman 2007).

Trifoliate orange is native to temperate China and Korea (Fig. 1; WHO 1998; Dianxiang & Mabberly 2008; Fang et al. 2011). The first known description of it in China and reference to its use as a rootstock occurs in the oldest known book on the orange, *Chū Lu* (Yen-Chih 1178). And in China, particularly, dried fruits of trifoliate orange have many medicinal uses (Duke & Ayensu 1985; PFAF 2014). Perhaps because of its uses in medicine and as a grafting rootstock, it was early cultivated in Japan (see below). Recent floristic treatments for Japan (e.g., Ohwi 1965; Walker 1976; Ohba 1999; Yamashita 2013) have not explicitly described it as naturalized there — Ohba (1999) noted only this: "Widely cultivated for hedges, stock for *Citrus*, and for medicine." — but André (1885) noted that it grew spontaneously in Japanese woods and that it had earlier been found there by Siebold and Burger and by Savatier.

Trifoliate orange also is known to be naturalized in Australia and Europe (Randall 2011) as well as the Kashmir Valley of northern India (Aslam et al. 2010). It is included in the Flora of Pakistan (Din & Ghazanfar 1980) but noted there to be "usually cultivated as an ornamental."

Variants

"The trifoliolate orange shows surprisingly few [horticultural] variations considering that it has been grown in China for thousands of years and in Japan since at least the eighth century" (Swingle & Reece 1967). A mutant with flattened and contorted stems, curved spines, and linear leaves (Flying Dragon, *Poncirus trifoliata* var. *monstrosa*) is popular in horticulture and was introduced into the USA from Japan in 1915. It is a dwarf variety usually cultivated as a potted plant and also used as rootstock especially for other potted *Citrus* varieties (Koskinen 2011).

Figure 1. Distribution of *Citrus trifoliata* in China and Korea. Some of the area may represent naturalized occurrence. Top: southeastern Asia, from Google Maps. Bottom: Outline of species distribution in China, from Fang et al. (2011), with South Korea added. Green star shows location of *Poncirus polyandra* — Yunnan Province, Kunming Prefecture, Fumin County.

A number of selections of *Citrus trifoliata* were identifed by Shannon et al. (1960) based on differences in origin, growth habit, and leaf or flower morphology, but these traits are significantly influenced by environmental conditions. Two groups, however, have been generally recognized with respect to flower size. In California, smaller-flowered plants become dormant earlier, which may be associated with greater cold resistance when used as a rootstock. Smaller-flowered selections of trifoliate orange also are less vigorous than larger-flowered types and are more bushy (Koskinen 2011). "In California, where dwarfing citrus rootstocks have been widely used, 8-to-12-year-old navel and Valencia oranges, Minneola tangelos, and Dancy tangerines on Rubidoux [small-flowered] trifoliate orange rootstock at different sites ranged from 10 to 14 feet tall. Comparable trees on Pomeroy [large-flowered] trifoliate rootstock were predicted to be 15%-20% taller, about 12 to 17 feet (Ferguson et al. 2004). In Japan, the larger-flowered forms also are considered to be more dwarfing (Bitters 1964).

Most modern accessions of trifoliate orange in the USA apparently have originated from early-imported lines by mutation or self-pollination. Based on polymorphic ISSR markers, Fang et al. (1997) found that 48 accessions clustered in four major groups, with most accessions falling into 2 groups — one group (24 accessions) included all large-flowered selections, the other (20 accessions) all small-flowered selections, including the Flying Dragon and a tetraploid (see below). One of the smaller groups was distinct in its loss of diversity and is perhaps derived from the small-flowered group. The other small group included accessions recently introduced from China.

Hardiness and associated use as a rootstock

Citrus trifoliata is said to survive temperatures as low as -13° F in Missouri (Porter 1972) and 3° F in Georgia (Ferguson et al. 2004). Edgar Anderson (1932) reported that a plant of trifoliate orange had been grown outside in Jamaica Plain, Massachussetts, and had regularly fruited — it was cultivated by Alfred Rehder in a protected place in a corner by the north wall of his home. Anderson also noted that plants had occasionally been seen growing without protection as far north as New York City. As mapped below, however, trifoliate orange is reported to naturalize in eastern Pennsylvania but not further north into New York.

Because of its hardiness, trifoliate orange has been used as a rootstock for grafting other species and varieties of *Citrus* and as a parent of novel cold-hardy varieties. Ferguson et al. (2004) noted, however, that "In north Florida, unseasonably warm temperatures higher than 70° F day/50° F night ... can reduce the freeze hardiness of trifoliate orange rootstocks. Trifoliate orange therefore may not be a consistently freeze hardy rootstock."

Trifoliate orange has long been the most important rootstock in Japan, primarily for satsuma mandarins, and is increasingly being employed in Australia, California, and Argentina (Koskinen 2011). A Florida nursery (JF&E 2014) currently uses three Trifoliate rootstocks: Flying Dragon (a dwarfing rootstock), Large Flower Trifoliate (a semi-dwarfing rootstook), and the vigorous Swingle.

Among *Citrus* species, trifoliate orange is the only one deciduous, which is significant in maintaining winter dormancy when used as a rootstock for other species. This also accounts for the more northern and temperate natural range of the species and perhaps for why it does not naturalize in warmer, more tropical climates.

Biology

Poncirus and its close relatives *Fortunella* and *Citrus reticulata* are facultatively apomictic (Garcia-Lor et al. 2013), seed production described as through adventitious embryony (Solntseva 1983), the seeds polyembryonic, containing both sexual and apomictic embryos (Fang et al. 1997). Khan and Roose (1988) observed that about 80–90% of seedlings from open-pollinated trifoliate orange seeds develop from apomictic embryos. Ferguson et al. (2004) noted that "In one report, seed

from Flying Dragon trees grown in four different locations produced between 0% and 75% zygotic [of sexual origin] seedlings. Researchers also found that the percentage of Flying Dragon [asexual and sexual] seedlings fluctuated greatly from year to year on the same tree." Self-compatibility facilitates production of sexual embryos.

Ability of solitary plants to reproduce has been confirmed by field observations — trifoliate orange was noted to be "apparently self-seeding" at an old farmhouse site in Polk Co., Texas (21 Mar 1957, *Traverse 321*, BRIT); Serviss (2014) also observed that it can set fruit without cross pollination.

Seed dispersal is described in various literature as through birds and other animals, but "seedlings will germinate from rotten fruits without dispersal or mechanical breach of the pericarp" (Serviss 2014). Where the species forms dense colonies, at least a significant portion of the recruitment is through seeds (Serviss, pers. comm.). One recent internet observer reported that fruits produced an average of 30 seeds. Trifoliate orange also reproduces by basal sprouting and root suckers.

Plants of trifoliate orange in England are described as relatively short-lived, deteriorating after about 25 years (Davis 1990), but at the Missouri Botanical Garden (St. Louis, Missouri), some individuals apparently reached almost 50 years in age (Porter 1972), limited in age by the cold winters. Individuals can reach 4–5 feet tall in 10 years and ultimately can grow to about 12 feet. Various internet nursery sites and discussions apparently have observed even more vigorous growth, reporting that it can grow up to 8–10 feet tall, rarely to 20 feet, and can reach 6 feet in 3 years. Trifoliate orange has been reported to begin flowering and fruiting when 3–4 years old or as late as 10–12 years old. Seedlings and a sapling are shown in Figures 4 and 5.

A tetraploid ($2n = 36$) of *Citrus trifoliata* was discovered in Jiangsu Province in 1974 (Chen & Liang 1989; Chen & Song 1989). It is faster-growing than the diploids and has thicker stems and smaller and more irregularly shaped fruits, and the seeds are fewer and with reduced viability.

***Poncirus polyandra* from Yunnan Province**

A second trifoliolate species has recently been described from Yunnan Province: *Poncirus polyandra* S.Q. Ding et al. (Ding et al. 1984). It is thought to be extinct in the wild — the only living plants are cultivated in several localities with reproduction monitored by botanists at the Kunming Institute of Botany (GONGxun 2013). Pang et al. (2007) and Li et al. (2010) found evidence confirming the distinction of *P. polyandra* from *P. trifoliata* and its independent origin (without an indication that *P. trifoliata* was involved in hybrid parentage of *P. polyandra*).

Phylogenetic and taxonomic position of the genus

Trifoliate orange has been treated in *Poncirus*, apart from *Citrus*, differing from the latter in its cold-hardiness, discontinuous pith (as transverse plates), deciduous, 3-foliolate leaves, flowers borne on old wood in early spring rather than on shoots of the season, basally free stamens, densely pubescent fruits, and pulp vesicles containing oily drops and having hair-like appendages (Bailey 1949, p. 609). Recent molecular studies, however, have generally indicated that *Poncirus* evolved from within the larger evolutionary nexus of *Citrus* (Araújo et al. 2003; Bayer et al. 2008; Penjor et al. 2013; Garcia-Lor et al. 2013), thus trifoliate orange is the more appropriately identified within the genus *Citrus*. Barkley et al. (2006) found that *Fortunella* clusters within *Citrus* but that *Poncirus* is sister to *Citrus*. Li et al. (2010) also found *Poncirus* sister to *Citrus* but species of *Fortunella* were not included in their analysis. Within *Citrus* sensu lato, the closest relatives of *Poncirus* are *Citrus reticulata* and species of *Fortunella* (Garcia-Lor et al. 2013).

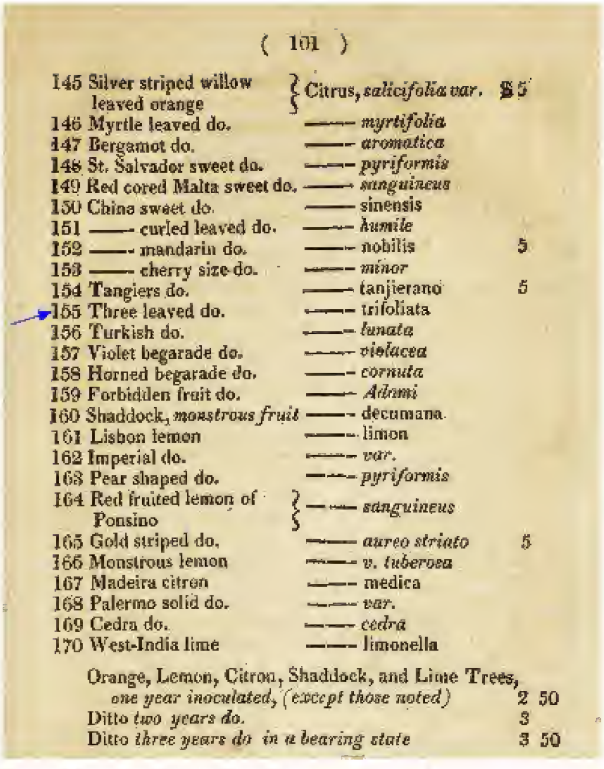
Figure 2. *Citrus triptera* Desf. (= *C. trifoliata*), from Andre (1885).

Trifoliate orange freely hybridizes with other *Citrus* species and was used in the USDA citrus breeding program, beginning in Florida in 1897 and continuing for several decades. This work produced a series of hybrids — (x kumquats (*Fortunella*) = citrumquats, x sweet oranges = citranges, x pummelos = citrumelos, x mandarins = citrandarins, x lemons = citremons, and x sour oranges = citradias) (Swingle & Reece 1967).

Citrus trifoliata L., Sp. Pl. ed. 2, 1101. 1763. *Poncirus trifoliata* (L.) Raf., Sylva Tellur. 143. 1838. *Bilacus trifoliata* (L.) Kuntze, Revis. Gen. Pl. 1: 99. 1891. TYPE: Protologue: "Habitat in Japonia." LECTOTYPE (designated by W. T. Swingle in Webber & Batchelor (ed.), *Citrus Industry* 1: 368. 1943): *"Karatats banna"* in Kaempfer, Amoen. Exot. Fasc., 801, 802. 1712.

Citrus triptera Desf., Tabl. École Bot., ed. 3 (Cat. Pl. Horti Paris.), 406. 1829.
Authorship of *Citrus triptera* often has been attributed to Ed. André (1885, see Fig. 2), but André himself appeared to recognize that *C. triptera* Desf. was the correct form of the name, in synonymy of that, he cited *Citrus trifoliata* L. and *Citrus trifolia* Thunb.

Citrus trifoliata var. **monstrosa** T. Itô, Encycl. Jap. (Nippon Hyakka Daijiten) 2: 1056. 1909. *Poncirus trifoliata* var. *monstrosa* (T. Ito) Swingle in Bailey, Stand. Cycl. Hort. 5: 2952. 1916.



(101)

145 Silver striped willow leaved orange	Citrus, *salicifolia var.*	$5
146 Myrtle leaved do.	—— *myrtifolia*	
147 Bergamot do.	—— *aromatica*	
148 St. Salvador sweet do.	—— *pyriformis*	
149 Red cored Malta sweet do.	—— *sanguineus*	
150 China sweet do.	—— sinensis	
151 —— curled leaved do.	—— *humile*	
152 —— mandarin do.	—— nobilis	5
153 —— cherry size do.	—— *minor*	
154 Tangiers do.	—— tanjierano	5
155 Three leaved do.	—— trifoliata	
156 Turkish do.	—— *lunata*	
157 Violet begarade do.	—— *violacea*	
158 Horned begarade do.	—— *cornuta*	
159 Forbidden fruit do.	—— *Adami*	
160 Shaddock, *monstrous fruit*	—— decumana	
161 Lisbon lemon	—— limon	
162 Imperial do.	—— *var.*	
163 Pear shaped do.	—— *pyriformis*	
164 Red fruited lemon of Ponsino	—— *sanguineus*	
165 Gold striped do.	—— *aureo striato*	5
166 Monstrous lemon	—— *v. tuberosa*	
167 Madeira citron	—— medica	
168 Palermo solid do.	—— *var.*	
169 Cedra do.	—— *cedra*	
170 West-India lime	—— limonella	

Orange, Lemon, Citron, Shaddock, and Lime Trees, *one year inoculated, (except those noted)*	2 50
Ditto *two years do.*	3
Ditto *three years do in a bearing state*	3 50

Figure 3 Listing of *Citrus trifoliata* in William Prince's 1823 "Catalogue of fruit and ornamental trees and plants, bulbous flower roots, green-house plants, &c. &c., cultivated at the Linnaean Botanic Garden" in Flushing, New York

Origin in the USA and distribution

Trifoliate orange was listed in William Prince's catalog (Prince 1823, Fig. 3, as *Citrus trifoliata*) of his Linnaean Botanic Garden in Flushing, New York, which sold many hundreds of woody and herbaceous species.

The species apparently was little noticed until it assumed a significant role in the U.S. Department of Agriculture citrus breeding program, as noted above. In 1869 William Saunders, (first botanist to be hired by the U.S.D.A. immediately upon its establishment in 1862) "was endeavoring to secure a hardy type of Japanese orange, and the trees froze in transit from San Francisco to Washington, but the stocks survived, and these proved to be the now well-known *P. trifoliata*. He enlisted the aid of the late Prof. P.J. Berckmans of Augusta, Georgia, in the work of saving the perpetuating this stock" (Brackett 1919, p. 1595).

In Texas, trifoliate orange was advertised as a hedge plant in the 1894 catalog of the Pearfield Nursery in Frelsburg (Colorado Co.) but was already in use for hedges at least by 1869 in Navasota (Grimes Co.) (Welch & Grant 2011).

Trifoliate orange was not included in any floristic accounts prior to 1900 or by Mohr (1901), Small (1903), or Small (1913). Perhaps the earliest published notice of its naturalization was Small (1933): "Woods and hammocks, Coastal Plain, Fla. to Tex. and Ga." Fernald (1950) observed that it was "Much used in the South for hedges, esc. to borders of woods, etc., Fla. to Tex. n. to e. Va." Even by 1968, it evidently was not known to be abundantly naturalized — Ahles (1968) noted that it was "Frequently cultivated, persistent about old home sites, less frequently escaped to thickets; Orange Co., N.C., Barnwell, Chester, Spartanburg cos., S.C. [Va., Miss.]."

Some of the oldest collections of naturalized plants mapped on Figure 6 are from areas close to large cities or universities, where plants presumably had been earlier cultivated: e.g., Travis Co., Texas (Austin, Univ. Texas); Pulaski Co., Arkansas (city of Little Rock); Knox Co., Tennessee (Knoxville, Univ. Tennessee); Pickens Co., South Carolina (Clemson Univ.). The oldest collections I have seen that reflect naturalizations are from Texas: Brazoria Co. (1910, TEX) and Travis Co. (1911, TEX).

"Large colonies [of trifoliate orange] are often observed in places where it is naturalized, and dense populations can be essentially impenetrable." In Arkansas, it is "capable of forming dense, thorny thickets which displace native plant species" (Serviss 2014). In the USA it grows in a wide range of habits, apparently on a correspondingly wide array of substrates. At least in southern Arkansas (Brett Serviss, pers. comm.) and in Walker Co., Texas (pers. observ.), it is an aggressive colonizer in bottomlands. In Fort Bend and Colorado counties, Texas, "it sometimes is the absolute dominant in the shrub layer of woodland mottes, especially those on sandy loam and dominated by whichever live oak entity is present" (Bill Carr, pers. comm.).

"When used as a rootstock, trifoliate orange can produce a standard-sized tree, about 15 feet tall, on clay and loamy soils and on shallow soils, but does not develop a deep or widely ranging root system and consequently is not drought tolerant. On deep, sandy, ridge soils, trees on trifoliate orange do not grow rapidly, making it a good candidate for close plantings with irrigation. It is poorly adapted to saline or calcareous conditions but is useful under wet conditions because of resistance to *Phytophthora* foot rot" (Ferguson et al. 2004).

Figure 4. Seedlings of trifoliate orange, probably first year.

Figure 5 Sapling of trifoliate orange, probably 2-3 years old

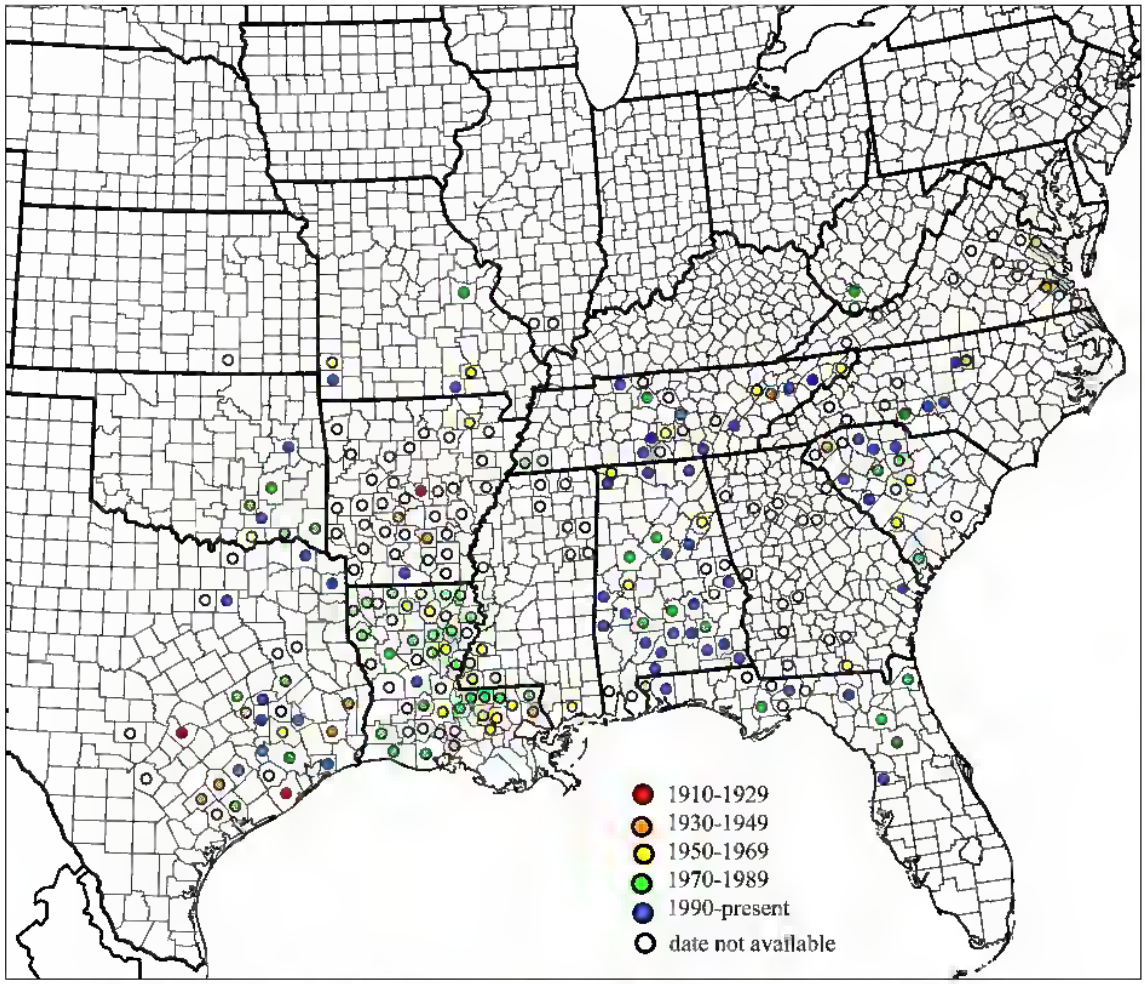


Figure 6. Distribution of *Citrus trifoliata* in the USA, with indication of time of naturalization. Dates are first collection for the county (see Appendix) The scattered locations of older collections suggests that the species has spread from multiple introductions. Concentration of 'green' in Louisiana and 'blue' in Alabama may reflect intensity of collecting programs, thus naturalizations probably were somewhat earlier. Undated records are from various sources and, because of incomplete or ambiguous label data, some may reflect persistent plantings rather than naturalized plants.

The apparent wide ecological amplitude suggests that differently adapted genotypes may be present. The ecological summary below for *Citrus trifoliata* derived from specimens examined in the current study

> Flowering (Mar–)Apr–May. Upland hardwoods, pine-hardwood, pine, beech-magnolia, and sweetgum woods, prairie openings, sandstone outcrops, hammocks over limestone, bottomlands, low pastures, streambanks and alluvial terraces, sandy floodplains, ditches, fencerows, roadsides, thickets in disturbed sites, especially in suburban areas, abandoned fields, rubbish dumps

Many excellent photos of trifoliate orange can be found on the internet. Especially see Serviss (2014).

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APPENDIX. *Citrus trifoliata*: first date of collection by county (documentation for Figure 6).

Alabama - Butler (2008), Calhoun (1967), Choctaw (1997), Colbert (2004), Coffee (2006), Conecuh (2006), Crenshaw (2009), Dale (2000), Escambia (1994), Hale (1967), Houston (1994), Jackson (1998), Jefferson (1985), Lauderdale (1969), Lee (2006), Limestone (1997), Lowndes (1988), Marengo (2009), Monroe (1997), Montgomery (2011), Pike (1989), Shelby (1996), Sumter (2006), Talladega (1992), Tuscaloosa (1979), Wilcox (1973)

Arkansas - Cleveland (1941), Hot Springs (1937), Lawrence (1968), Pulaski (1925), Union (1999)

Florida - Alachua (1980), Duval (1982), Escambia (1993), Hernando (2009), Leon (2010), Liberty (1982), Marion (1975), Santa Rosa (1993), Suwanee (2000)
Georgia - Bryan (1994), Echols (1967)

Louisiana - Ascension (1951), Bossier (1976), Caddo (1970), Calcasieu (1975), Caldwell (1973), Cameron (1977), Catahoula (1969), Claiborne (1972), Concordia (1975), DeSoto (1978), East Baton Rouge (1989), East Feliciana (1987), Evangeline (1978), Franklin (1981), Iberia (1938), LaSalle (1975),

Lincoln (1969), Madison (1980), Morehouse (1977), Natchitoches (1979), Ouachita (1968), Pointe Coupee (1972), Rapides (2003), St Helena (1971), St Landry (1968), St Tammany (1949), Tangipahoa (1957), Vermilion (1989), Washington (1983), West Carroll (1978), West Feliciana (1972), Winn (1981)

Mississippi - Harrison (1969), Jefferson (1966), Wilkinson (1966)

Missouri Carter (1958), Franklin (1973), Jasper (1959), Newton (2004), Oregon (2003)

North Carolina - Alamance (2011), Mecklenberg (1975), Montgomery (2000), Orange (1943), Stanly (2007)

Oklahoma - Atoka (2001), Bryan (1962), Choctaw (1989), Cleveland (cultivated), Coal (1973), McCurtain (1973), Muskogee (1994), Payne (cultivated), Pittsburgh (1973)

South Carolina - Abbeville (2000), Barnwell (1953), Chester (2003), Edgefield (1997), Fairfield (1983), Jasper (1983), Newberry (1986), Pickens (1931), Richland (1967), Spartanburg (2009), Union (1993)

Tennessee - Anderson (1966), Bedford (1965), Bledsoe (1963), Cannon (2004), Carter (1956), Davidson (1989), Fayette (1981), Giles (2004), Greene (2001), Jefferson (1991), Knox (1936), Marion (2005), Marshall (2003), Meigs (2003), Montgomery (2000), Shelby (1972)

Texas - Anderson (1964), Brazoria (1910), Brazos (1949), Chambers (1990), Dewitt (1942), Colorado (1996), Dallas (1998), Grimes (1992), Hardin (1947), Harris (1979), Houston (1979), Jackson (1982), Jasper (1948), Lavaca (1937), Madison (1998), Montgomery (1968), Red River (1993), Robertson (1979), San Jacinto (1992), Travis (1911), Victoria (1963), Waller (1993)

Virginia - Essex (1941), Spotsylvania (1939), Surry (1938)

West Virginia - Wyoming (1972)

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NOTEWORTHY RECORDS FROM DARE AND TYRRELL COUNTIES, NORTH CAROLINA

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ABSTRACT

Dare and Tyrrell counties, North Carolina, were inventoried in 2012-13 for natural areas and rare species. New county records and recent collections of scarce taxa are documented here (89 taxa). These records improve understanding of the distribution of the flora of North Carolina.

Since the landmark publication of the Manual of the Vascular Flora of the Carolinas by A.E. Radford, H.E. Ahles, and C.R. Bell (1968), botanical exploration and documentation have continued apace. The Coastal Plain, comprising roughly 45% of North Carolina, has been the subject of many papers and graduate theses documenting the region's flora. Among them are a number which treat portions of Dare and Tyrrell counties: Brown (1959), Burk (1961), Clark et al. (in press), Crutchfield (1964), Faucette et al. (in prep.), Gaddy (1985), Krings (2010), Levy (1976), Sorrie (2014a, 2014b), and Stalter and Lamont (1997).

Dare and Tyrrell counties are situated at the eastern end of the Albemarle Peninsula in northeastern North Carolina, surrounded on three sides by large estuaries locally called sounds (Figs. 1 and 2). Because of the lengthy barrier beach/dune/marsh system of the Outer Banks and the large number of maritime microhabitats, Dare County is acknowledged as a critical meeting ground of northern and southern flora and fauna and is critical to the state's biodiversity (Sorrie 2014a). The vast peatlands of mainland Dare County and adjacent Tyrrell County harbor a whole suite of natural communities and species absent from the barrier islands (McDonald & Ash 1981; Peacock & Lynch 1982; Sorrie 2014a, 2014b). Between them, the two counties harbor about 1000 vascular species and major infraspecific taxa, about 25% of the state flora. While this number is modest compared to most counties of the North Carolina Coastal Plain, Dare and Tyrrell harbor a significant number of local, regional, and state rarities, including 62 state-listed rare plant species in Dare and 19 in Tyrrell (Gadd & Finnegan 2012).

METHODS

The author conducted natural areas inventories of Dare and Tyrrell counties in 2012-13, which included two complete field seasons (Sorrie 2014a, 2014b). During the course of this work, emphasis was placed on locating and assessing the best remaining natural areas, including exemplary or rare natural communities, rare plants, and rare animals. Critical to this effort was a review of previous documents pertaining to the floristics and natural history of these counties. Many previously reported specimens were checked for correct determination at CAHA, DUKE, NCSC, and NCU.

Nomenclature follows Weakley (2012). For each taxon, the first known collection is cited; county of collection is Dare unless stated to be Tyrrell. Capitalized habitat descriptors are natural communities described in Schafale (2013). Specimens at Cape Hatteras National Seashore herbarium (CAHA) are each assigned a unique accession number by the National Park Service, provided here, so that even a specimen without a collector's number can be uniquely identified. "NCNHP database" is the official repository of rare species data at the North Carolina Natural Heritage Program in Raleigh.

Figure 1. Towns and major roads in Dare County, North Carolina.

Figure 2. Towns and major roads in Tyrrell County, North Carolina.

The following symbols are used throughout this paper.

+ = new to Dare County (per Radford, Ahles, and Bell range maps)
* = new to Tyrrell County (per Radford, Ahles, and Bell range maps)
$ = on North Carolina Rare Plant List (Gadd & Finnegan 2012)
# = on North Carolina Watch List (Gadd & Finnegan 2012).

RESULTS

AIZOACEAE

$ *Sesuvium maritimum* (Walt.) B.S.P. First known collection: Pea Island, dune depression ¾ mi S of Oregon Inlet, 25 Aug 1953, *Radford* (NCU). Given the large amount of suitable habitat on the Outer Banks, this species is unaccountably scarce and is on the NC rare list. A large population occurs on wet sandy flats at the interface between oligohaline marsh and impoundment pond at Pea Island National Wildlife Refuge (*Sorrie 13220* CAHA, NCSC, NCU). Dare County is the species' northern range limit.

APIACEAE

+ *Sanicula canadensis* L. var. *floridana* (Bickn.) H. Wolff. First known collection: Cape Hatteras, shady sandy soil, Jun-Jul 1898, *Ashe s.n.* (NCU). Based on material at NCU and NCSC, all Outer Banks specimens of this species prove to be this variety, which differs from the nominate in its smaller basal leaves and longer spines on leaf margins. A recent collection is from Buxton Woods, 11 Jun 2012, *Sorrie 12993* (NCU). This plant occurs in scattered small populations in Maritime Deciduous Forest and Maritime Evergreen Forest in Buxton Woods, Nags Head Woods, and Kitty Hawk Woods.

+ *Sanicula marilandica* L. First known collection: Nags Head Woods, Sep 1950, *Fox & Godfrey 2318* (NCSC). Recent collections are from Maritime Deciduous Forest at Nags Head Woods: *Krings 728 and 1082* (NCSC) and *Sorrie 13283* (NCU). In North Carolina, it is disjunct from Jones and Wake counties, a minimum of 160 km.

ASTERACEAE

Bidens discoidea (Torrey & Gray) Britt. First known collection: Nags Head Woods, Sep 1950, *Godfrey & Fox 51030* (NCSC). It has not been seen there since, but has been found to be locally numerous in Maritime Swamp Forest at Kitty Hawk Woods, 17 Sep 2013, *Sorrie 13241* (NCU).

+$ *Bidens trichosperma* (Michx.) Britt. Known from three populations recently discovered on the Dare mainland, including: Mashoes Marshes, locally common at roadside marsh, 16 Sep 2013, *Sorrie 13115* (NCU). There are two historical records from Tyrrell County.

+ *Carphephorus bellidifolius* (Michx.) Torrey & Gray. Roanoke Island, edge of loblolly pine-oak woods, Victor Meekins Road NW of Manteo, 11 Jul 2012, *Sorrie 13039* (NCU). Plants were numerous and grew with more than twenty species normally associated with longleaf pine uplands; the site appears to be a highly disturbed, remnant, pine-oak community.

+ *Liatris pilosa* (Ait.) Willd. First known collection: Kitty Hawk, *Bandle 453* (ODU) as cited by Krings (2010). It was reported from Nags Head Woods by Stalter and Lamont (1997) and is rare in sandy, dry oak-pine woods at Wright Brothers Memorial, 17 Sep 2013, sight record.

Liatris spicata (L.) Willd. var. *resinosa* (Nutt.) Gaiser. First known collection: edge of sapling cypress swamp on hwy 345, 3¾ mi N of Wanchese, Roanoke Island, 21 Sep 1940, *Radford & Stewart 884* (NCU). It is now locally common in moist clay-sand soil beside NC 345, 1 mi N of Wanchese, 8 Oct 2013, *Sorrie 13272* (NCU). Here plants grew with *Paspalum floridanum, P. praecox, Ionactis linariifolia, Hypericum cistifolium, Symphyotrichum simmondsii, Quercus marilandica*, and other species rare in Dare County.

Solidago arguta Ait. var. *caroliniana* A. Gray. Examination of specimens and additional field work confirm that all outer Coastal Plain plants of *S. arguta* are referrable to var. *caroliniana*, with its

much smaller and narrower basal leaves, narrower stem leaves, glabrous leaves, and strigillose cypselae. First known collection: Roanoke Island, open woods, Fort Raleigh, 31 Jul 1959, *Schallert 1960* (NCU). It is local in Maritime Deciduous Forest and Maritime Evergreen Forest in Jockey's Ridge State Park, Nags Head Woods, and Kitty Hawk Woods.

+ *Solidago petiolaris* Ait. First known collection: Nags Head Woods, Sep 1974, *Peterson s.n.* (CAHA). More recent collections, all from the same site, are several by Krings (cited in Krings 2010), and along Old Nags Head Woods Road, 31 Oct 2013, *Sorrie 13284* (NCU). Dare County is the northernmost range limit.

+ *Symphyotrichum simmondsii* (Small) Nesom. First known collection: Hatteras Island, 3 mi W of Old Cape Hatteras lighthouse, freshwater ponds and swales, 15 Oct 1940, *Fosberg 17970* (NCU). It occurs as scattered plants in Interdune Marshes S of Buxton Woods, 24 Oct 2012, *Sorrie 13127* (NCU), and also found in a moist grassy Interdune Marsh at the base of high dunes, Jockey's Ridge State Park, 30 Oct 2013, *Sorrie 13278* (NCU, NCSC). This species was not known to be a member of the North Carolina flora until Nesom annotated specimens from *S. dumosum* (L.) Nesom at NCU.

BETULACEAE

+ *Betula nigra* L. Discovered in a thicket of *Quercus virginiana* P. Miller and *Ilex vomitoria* Ait. beside Albemarle Sound, Corps of Engineers Research Facility N of Duck, several small trees, 26 Jun 2013, *Sorrie 13208* (NCU). This riparian species is undoubtedly adventive here.

CARYOPHYLLACEAE

Silene gallica L. First known collection: roadside between Hatteras and Buxton, 6 Jun 1959, *Burk b6-7* (NCU). Burk (1961) noted that it also occurred on Bodie Island. Today this alien is restricted to the same area, all south of Nags Head town, in open Stable Dune Barrens, Maritime Dry Grasslands, and roadsides (*Sorrie 12944* CAHA, NCU). It also was collected from Ocracoke Island, Hyde County, in 2005 (*LeBlond 6096* NCU).

+ *Stipulicida setacea* Michx. First recorded by M. Schafale, M. Buchanan, and S. Strickland on 2 Jul 2010 from a Stable Dune Barren at Wright Brothers Memorial (NCNHP database). It is also recorded on the Jockey's Ridge State Park plant list, and confirmed there in 2013: edge of live oak-loblolly pine woodland, 100+ plants, 28 Jun 2013, *Sorrie 13223* (NCU).

CISTACEAE

+$ *Crocanthemum carolinianum* (Walt.) Spach. Discovered in a Stable Dune Barren with *Hudsonia tomentosa* Nutt. and *Lechea maritima* Leggett ex B.S.P. var. *virginica* Hodgdon, Kitty Hawk Woods, 2 May 2013, *Sorrie 13153* (GH, NCSC, NCU). This represents a new northern range limit.

$ *Crocanthemum georgianum* (Chapm.) Barnhart. First known collection: open sandy spots, Cape Hatteras, Jun-Jul 1898, *Ashe s.n.* (NCU). It was recently documented as locally common on roadsides and disturbed areas, Lighthouse Road, Buxton, 1 Jun 2013, *Sorrie 13192* (CAHA, NCU).

CLADONIACEAE

+# *Cladina evansii* (Abbayes) Hale & Culb. This distinctive lichen is locally common in xeric sand of sand laurel oak-loblolly pine woods at Wright Brothers Memorial, 17 Sep 2013, *Sorrie 13243* (NCU). This represents a new northern range limit.

CONVOLVULACEAE

Calystegia soldanella (L.) R. Br. ex Roem. & Schult. There are no specimens at NCU nor NCSC to support the report in Radford, Ahles, and Bell (1968). Stalter and Lamont (1997) reported it from "ocean dunes near Kitty Hawk." Krings and I found it to be rare and local on a foredune at Cape Hatteras Point, 19 Sep 2013, *Sorrie 13254* (NCU). This species is considered non-native in North Carolina by Weakley (2012) and in Virginia by Weakley, Ludwig, and Townsend (2012).

CYPERACEAE

+ *Carex arenaria* L. This alien sedge was previously known from Carolina Beach State Park in New Hanover County, North Carolina, and also eastern Maryland and southeastern Virginia (Weakley 2012). A single Dare County specimen exists: no location, 30 Jul 1990, *Stalter & Lamont s.n.* (CAHA 2664).

+$ *Carex basiantha* Steud. First known collection: Nags Head, Apr 1898, *Ashe s.n.* (NCU). This specimen lay unidentified until 2011.

$ *Carex calcifugens* Naczi. First known collection: near Cape Hatteras, 16 Jun 1898, *Ashe s.n.* (NCU). This maritime and near-maritime species proves to be frequent in Maritime Evergreen Forest and Maritime Deciduous Forest from Buxton Woods north to Kitty Hawk Woods. Recent collections include: Nags Head Woods, 19 Apr 2012, *Sorrie 12929* (GH, NCSC, NCU, NY) and Buxton Woods, 15 May 2012, *Sorrie 12946* (CAHA, MO, NCU). Dare County is the species' northern limit.

+*$ *Carex canescens* L. var. *disjuncta* Fernald. First known collection: Tyrrell County, swamp on E side of SR 1105, with *Carex stricta*, 23 Apr 1984, *Leonard 8363* (FSU). Robust tussocks occurred at the same site in 2012 (*Sorrie 12915* NCSC, NCU) and along NC 94 well to the south (*Sorrie 12920* NCSC, NCU). It also was found in Tyrrell County on a Floating Bog along New Lake Fork of Alligator River, 30 May 2013, *Sorrie 13177* (NCU, NY). On the Dare County mainland, it was common along Milltail Creek, 29 May 2013, *Sorrie 13172* (NCU).

Carex kobomugi Owhi. This alien was reported from Bodie Island, "coastal dunes and swale at campground N of Oregon Inlet" by Stalter and Lamont (1997), but their specimen has not been located. Three collections from here and elsewhere on Bodie Island (CAHA 1310, 4575, 4733) all prove to be *C. pumila* Thunb. Thus there is no verified record of *Carex kobomugi* in North Carolina south of Currituck County.

Carex pumila Thunb. First known collection: Hatteras Island, 1959, *Burk b49-18* (NCU). Recent collections suggest that this alien is spreading: Bodie Island, Cape Hatteras National Seashore, 100 meters S of Whalebone Junction, 19 May 1992, *Reznicek 8935* (NCU); locally common on backside of foredune, Coquina Beach, Cape Hatteras National Seashore, 31 May 2013, *Sorrie 13184* (NCU); and on backdunes at Corps of Engineers Research Facility N of Duck, 26 Jun 2013, *Sorrie 13204* (NCU).

+# *Cyperus surinamensis* Rottb. First known North Carolina collection: New Hanover County, Silver Lake, 16 Aug 2002, *LeBlond 5668* (NCU). In Dare County it was common in road margins at Cape Hatteras Point campground, Cape Hatteras National Seashore, 12 Jun 2012, *Sorrie 13009* (CAHA, NCU). Weakley (2012), unaware of the NC specimens, has treated it as native in southern South Carolina. I suggest treating the North Carolina populations as adventive, as there are no occurrences in any natural Maritime Wet Grassland communities — habitats where this species would be expected to grow.

+$ *Cyperus tetragonus* Ell. First recorded by A. Weakley along Flowers Ridge Road, Buxton, 13 Nov 1987 (NCNHP database). This tall flatsedge is frequent along trails and on slopes in Maritime Evergreen Forest in Buxton Woods, 16 Aug 2012, *Sorrie 13077* (CAHA, NCU). This represents a new northern range limit.

$ *Eleocharis cellulosa* Torrey. First known collection: 3 mi W of Cape Hatteras lighthouse, ponded swale, 15 Oct 1940, *Fosberg* (NCU). It is the dominant plant here, covering a few hectares, 19 Sep 2012, *Sorrie 13102* (CAHA, NCU); and also locally common on mainland Dare County along Mashoes Road at the edge of a Tidal Freshwater Marsh, 16 Sep 2013, *Sorrie 13233* (NCSC, NCU).

+ *Eleocharis fallax* Weatherby. This species included *E. ambigens* Fernald in Radford, Ahles, and Bell (1968). The discovery of large populations of this rare and little known species in 2012 and 2013, and its distinctiveness from *E. ambigens*, are discussed in a separate paper (Sorrie & LeBlond 2014). Dare County records are from Interdune Marshes and Maritime Wet Grasslands, vouchered by *Sorrie 12995* (NCU), *13002* (CAHA, NCU), and *13187* (GH, NCU). LeBlond collected it in 1996 from Onslow County in a Tidal Red Cedar Forest (cited in Sorrie and LeBlond 2014). These records represent a new southern range limit.

+$ *Eleocharis montevidensis* Kunth. First known collection: in wet meadows, Cape Hatteras, 16 Jun 1898, *Ashe s.n.* (NCU), specimen originally misidentified as *E. tricostata* Torrey. It occurs at margins of Maritime Wet Grasslands between Frisco and Buxton, 15 May 2012, *Sorrie 12948* (CAHA, NCU). This represents a new northern range limit.

+ *Furena breviseta* (Coville) Coville ex Harper. In Radford, Ahles, and Bell (1968) this species was synonymized under *F. squarrosa* Michx. First known collection: Roanoke Island, freshwater marsh 0.5 mi N of Wanchese, 2 Sep 1959, *Crutchfield 4694* (NCU).

*$ *Isolepis carinata* Hook. & Arn. ex Torrey. Discovered new to Tyrrell County in the moist grassy bed of Davis Canal Road W of NC 94, 18 Apr 2012, *Sorrie 12919* (NCSC, NCU). Here it is disjunct at least 220 km from the nearest North Carolina collections in Durham and Pender counties.

+ *Kyllinga gracillima* Miquel. Discovered new to Dare County by Clark et al. (in press): moist edge, Kitty Hawk Woods, *Clark 370* (NCSC). Also local on a moist grassy roadside and margin of Tidal Freshwater Marsh, with *Bidens trichosperma*, Mashoes Road, 16 Sep 2013, *Sorrie 13231* (GH, NCSC, NCU). This species, also known as *Cyperus brevifolioides* Thieret & Delahoussaye, was previously known in North Carolina only from two mountain counties but recorded in South Carolina from Charleston County and "infrequent throughout" Virginia (Weakley, Ludwig, & Townsend 2012).

$ *Rhynchospora microcarpa* Baldwin ex A. Gray. First known collection: 3 mi W of Old Cape Hatteras lighthouse, freshwater swale, 15 Oct 1940, *Fosberg 17987* (NCSC). Scattered plants inhabit wet exposed soil of Interdune Marshes S of Buxton Woods, 19 Sep 2012, *Sorrie 13105* (NCSC, NCU) and 24 Oct 2012, *Sorrie 13125* (GH, NCU). This represents a new northern range limit.

+$ *Rhynchospora odorata* C. Wright ex Griseb. Several populations inhabit Maritime Wet Grasslands in the vicinity of Cape Hatteras Point, with *Rhynchospora colorata* (L.) H. Pfeiffer, *Scleria verticillata* Muhl. ex Willd., *Dichanthelium neuranthum* (Griseb.) LeBlond, and *D. caerulescens* (Hackel ex Hitchc.) Correll, 11 Jun 2012, *Sorrie 12994* (CAHA); 19 Sep 2012, *Sorrie 13109* (NCU); and 25 Oct 2012, *Sorrie 13128* (NCSC). This represents a new northern range limit.

+$ *Schoenoplectus etuberculatus* (Steud.) J. Sojak. Collected from a "small shallow wetland just N of Jennette Sedge, with *Eleocharis montevidensis* and *Nymphaea odorata*," 12 Jul 1984, *Gaddy 253* (CAHA 1314).

Scleria flaccida Steud. In Radford, Ahles, and Bell (1968) this species was synonymized under *S. triglomerata* Michx. First known collection: sandy openings in woods of *Pinus taeda* and *Quercus virginiana*, Peter's Bridge, Hatteras Island, 14 Oct 1940, *Fosberg 17874* (NCU). LeBlond (in Weakley 2012) recognized this robust, broad-leaved taxon of the outer Coastal Plain as distinct from *S. triglomerata*, and I concur, as it has a more robust gestalt, different habitat, and maritime/near-maritime range. It is frequent to common in dry to mesic Maritime Evergreen Forest in Buxton Woods, apparently the northern range limit: 15 May 2012, *Sorrie 12945* (CAHA, NCU).

*$ *Scleria verticillata* Muhl. ex Willd. Discovered new to Tyrrell County in the wet margin of route 94, S of Northwest Fork of Alligator River, 13 Aug 2012, *Sorrie 13065* (NCSC, NCU). It is also documented from several populations in Maritime Wet Grasslands in the vicinity of Cape Hatteras Point, Dare County (NCNHP database).

EQUISETACEAE

+ *Equisetum arvense* L. First known collection: Tyrrell County, roadside, New Lake Fork of Alligator River near NC 94, 18 May 1958, *Radford 33891* (NCU). Elsewhere in Tyrrell it is common at the edge of a Nonriverine Swamp Forest, Grapevine Landing Road, 13 Aug 2012, *Sorrie 13061* (NCU). In Dare County, it is known only from moist sandy woods margin, W of the Navy Bombing Range, 26 Apr 1984, *Leonard 8375* (NCU).

ERICACEAE

+# *Gaylussacia bigeloviana* (Fernald) Sorrie & Weakley. In Radford, Ahles, and Bell (1968) this taxon was synonymized with *G. dumosa* (Andrews) Torrey & Gray. First known collection: pocosin on US 264, near Manns Harbor, 23 May 1954, *Radford 8200* (NCU). A recent collection is from a Low Pocosin NE of Pain's Creek, 15 Jun 2012, *Sorrie 13021* (GH, NCSC, NCU). It is an uncommon inhabitant of Low Pocosins in peatlands of Bladen, Brunswick, Carteret, Dare, and Pender counties, North Carolina, and at a streamhead seepage swamp in Lexington County, South Carolina. These southernmost stations are disjunct from southern Delaware.

EUPHORBIACEAE

+$ *Euphorbia ammanoides* Kunth. Reported from Bodie Island by Johnson (1992, as *Chamaesyce ingallsii* Small), but it is unclear if specimens were taken. It is frequent in stable and semistable sand of Dune Grass and Maritime Dry Grassland communities on Bodie and Hatteras Islands, where it far outnumbers *E. polygonifolia* L.: 18 Sep 2012, *Sorrie 13093* (CAHA, NCSC, NCU); same date, *Sorrie 13100* (CAHA, GH, NCU).

FABACEAE

+ *Lotus corniculatus* L. The first known report is by Stalter and Lamont (1997): "roadside N of Rodanthe, rare." It is now common and spreading on Hatteras Island along NC 12 S to Buxton: 31 May 2013, *Sorrie 13185* (NCSC, NCU).

+ *Sesbania herbacea* (P. Mill.) McVaugh. Some 40 fruiting plants were found at the junction of Long Curve Road and Lake Worth Road, Stumpy Point, 1 Nov 2013, *Sorrie 13287* (NCU).

IRIDACEAE

$ *Iris prismatica* Pursh ex Ker Gawl.. First known collections: ditch on NC 345, 1.5 mi S of Manteo, 16 May 1959, *Crutchfield 3569* (NCU); Wanchese Road [NC 345], wet area, 19 May 1976,

Dunes of Dare Garden Club s.n. (CAHA 966). A few plants still occur here in a roadside ditch, 31 May 2013 (NCNHP database).

Iris verna L. var. *verna*. First known collection: Roanoke Island, roadside ditch 1.7 mi N of Manteo, 17 Apr 1959, *Crutchfield 2997* (NCU). This remains the only collection from off the mainland of North Carolina.

+ *Sisyrinchium angustifolium* P. Mill.. First known collection: common in Maritime Wet Grassland, Jockey's Ridge State Park, 29 Apr 2013, *Sorrie 13141* (NCSC, NCU). It was also seen in an Interdune Marsh in Buxton and a Maritime Wet Grassland near Frisco, both in 2012.

+* *Sisyrinchium rosulatum* Bickn. Burk (1961) reported it from Hatteras Village, but the specimen (*Burk b45-10*, NCU) actually is *S. atlanticum* Bickn. Crutchfield (1964) reported it (as *S. brownei* Small) from a roadside in Wanchese (*Crutchfield 3611*), but the specimen is not at NCU. First known Dare County collection: along route 12 between Whalebone Junction and Oregon Inlet, 19 May 1985, *Davison s.n.* (CAHA 1051). First known Tyrrell County collection: grassy roadside of SR 1117, 17 Apr 2012, *Sorrie 12911* (NCSC, NCU). Today this species is frequent on roadsides and lawns throughout both counties.

LAMIACEAE

$ *Pycnanthemum setosum* Nutt. First known collection: Tyrrell County, freshwater marsh near NC 94, 3.1 mi S of Kilkenny, 6 Aug 1958, *Radford 39276* (NCU). Recent Tyrrell collections are from Cove Landing Road, 25 Jun 2013, *Sorrie and Jackson 13202* (NCU); and marshy ditch by US 64, E of Columbia, 16 Sep 2013, *Sorrie 13230* (NCU).

+* *Stachys floridana* Shuttlew. ex Benth. First known collection: Dare County, edge of Doctor's Hill Road, Buxton Woods, 15 May 2012, *Sorrie 12955* (NCU). In Tyrrell County, seen in flower along Bee Tree Trail, Pettigrew State Park, 28 May 2013. This alien species was unknown in North Carolina when Radford, Ahles, and Bell (1968) was published, but now is scattered across the state.

PHYTOLACCACEAE

+# *Phytolacca rigida* Small. This taxon was not recognized by Radford, Ahles, and Bell (1968). First known collection: waste place, Buxton Woods, *Radford 7565* (NCU). It occurs sporadically in Dare County from Buxton north to Duck, where a collection was made from a roadside on the S side of town, 17 Sep 2012, *Sorrie 13092* (NCU).

PINACEAE

+ *Pinus nigra* Arn. Prior reports of *P. pinaster* Ait. and *P. thunbergiana* Franco (Burk 1961; Weakley 2012) are not substantiated by vouchers at NCU. Using the key in Haines (2011), specimens collected from the large plantation on Hatteras Island south of Salvo prove to be *P. nigra* (*Sorrie 13186* NCU; *13218* NCU). The cones are sessile and the shoot tips are viscous-sticky, characters in line with *P. nigra*. Additional plantings and escaped individuals occur north to Southern Shores.

PLANTAGINACEAE

+$ *Limosella australis* R. Br. First known collection: marsh on Currituck Sound near Caffey's Inlet, 3 Jun 1951, *Radford 5756* (NCU). The specimen label says Currituck County, but Caffey's Inlet straddles the line and the old Life Saving Station was actually in Dare County. It is reported as occurring at Jockey's Ridge State Park (park list of plants).

POACEAE

Aira praecox L. First known collection: roadside, Hatteras Village, 12 May 1960, *Burk b45-27* (NCU). At the time, this was the sole record for North Carolina. A second collection was made in the 1980s on Bodie Island: *Davison s.n.* (CAHA 3854). Recently it was collected on a roadside near Coquina Beach, Bodie Island, 31 May 2013, *Sorrie 13183* (CAHA, NCU). This inconspicuous and epemeral alien is likely more widespread.

+ *Andropogon glaucopsis* Ell. This species was synonymized within *A. virginicus* L. in Radford, Ahles, and Bell (1968). First known collection: Roanoke Island, edge of pine stand 0.3 mi N of Wanchese, 17 Oct 1959, *Crutchfield 5128* (NCU). It was mapped for Tyrrell County by Blomquist (1948), the specimen presumably at DUKE. It is common on mainland Dare and Tyrrell counties in wet openings in Pond Pine Woodland, High Pocosin, and Low Pocosin. In Dare County, Outer Banks populations have been seen in Interdune Marshes and Maritime Wet Grasslands at Buxton Woods, Jockey's Ridge State Park, and Duck.

+* *Andropogon temuispatheus* (Nash) Nash. [= *A. glomeratus* (Walter) B.S.P. var. *pumilus* Vasey ex Dewey]. This species was synonymized within *A. virginicus* L. in Radford, Ahles, and Bell (1968). All collections from the Outer Banks that were originally determined to be *A. glomeratus* (NCU, NCSC) are instead *A. tenuispatheus*, due to: plant taller, inflorescence longer, inflorescence with more branches, inflorescence branch clusters curved or rounded distally (vs. flat-topped or truncate), shorter ligules, shorter raceme sheaths, and maritime/near maritime habitats (vs. freshwater seepage slopes and wet pine savannas). First known collection: sand flat at Avon, 10 Oct 1953, *Radford 7745* (NCU). It is *A. tenuispatheus*, and not *A. glomeratus* sensu stricto, which is colonizing inland roadsides and fields throughout the South.

+# *Aristida lanosa* Muhl. ex Ell. First known collection: top of stable dune behind live dune, Nags Head forest, 22 Oct 1960, *Burk b58-15* (NCU). This specimen was originally misidentified as *A. condensata* Chapm. Recently it was collected in Nags Head Woods by Krings (*2421 and 2422* NCSC).

+ *Bromus rigidus* Roth. First known collection: Buxton, sandy roadside near Orange Blossom Bakery, 20 Jul 1989, *Davison s.n.* (CAHA 3859). This alien was collected recently on a disturbed margin of Old Doctor's Road, Buxton, 15 May 2012, *Sorrie 12957* (NCSC, NCU). Many plants were also noted in disturbed sand at the Corps of Engineers Research Facility north of Duck, 26 Jun 2013.

+# *Chasmanthium sessiliflorum* (Poir.) Yates. First known collection: mixed hardwoods, Kitty Hawk, 4 Aug 1966, *Radford & Pence 45097* (NCU). It is abundant in Maritime Evergreen Forest in Buxton Woods, *Sorrie 13034* (CAHA, NCSC, NCU, US) and locally common in Maritime Deciduous Forest in Kitty Hawk Woods, *Sorrie 13239* (NCU).

+ *Cortaderia selloana* (J.A. & J.H. Schult.) Asch. & Graebn. This alien is widely planted in the state but rarely reported as escaped or established. Plants can be found in scattered roadside and open woodland locations from Buxton to Hatteras Village (sight records).

+* *Dichanthelium arenicolo*ides (Ashe) LeBlond comb. nov. in prep. This species was not recognized at any rank within *Panicum* in Radford, Ahles, and Bell (1968). First known collection: open place near Fort Raleigh, Roanoke Island, 30 Jul 1959, *Schallert 5023* (NCU). It was mapped for Tyrrell and Currituck counties by Blomquist (1948) and the specimens presumably are at DUKE. Plants form distinctive circular mats similar to *D. aciculare* (Desv. ex Poir.) Gould & Clark, but with longer leaves and longer spikelets. It is common in open Stable Dune Barrens throughout the Outer Banks. Recent collections include the Corps of Engineers Research Facility N of Duck, 11 Jul 2012,

Sorrie 13036 (NCU); Stable Dune Barrens at Wright Brothers Memorial, 15 Aug 2012, *Sorrie 13072* (NCSC, NCU); and dunes just S of Buxton Woods, 24 Oct 2012, *Sorrie 13122* (CAHA, NCU).

Dichanthelium boscii (Poir.) Gould & Clark. First known collection: Nags Head Woods, Jun 1950, *Fox and Godfrey 2316* (NCSC). Recently collected from mesic slopes in Buxton Woods, 27 Jun 2013, *Sorrie 13213* (NCSC, NCU). It is frequent in Maritime Deciduous Forest and Maritime Evergreen Forest at Buxton Woods, Nags Head Woods, and Kitty Hawk Woods.

+$ *Dichanthelium caerulescens* (Hackel ex Hitchc.) Correll. This species was not recognized at any rank within *Panicum* in Radford, Ahles, and Bell (1968). First known collection: marsh at Cape Hatteras, 26 Aug 1953, *Radford 7627* (NCU). There are 9 current populations in Dare County, all from Maritime Wet Grasslands on Hatteras and Pea Islands (NCNHP database). Collections include Pea Island National Wildlife Refuge, swale behind dunes, 4 Jun 2003, *Carolina Vegetation Survey* (NCU); Cape Hatteras Point campground, 12 Jun 2012, *Sorrie 13003* (NCU); and beach access ramp 49 E of Frisco, 19 Sep 2013, *Sorrie 13256* (CAHA, DUKE, NCU, NY).

+$ *Dichanthelium fusiforme* (Hitchc.) Harvill. First known collection: Run Hill, top of dune, about 205 meters W of junction of Tenth Street and West Corrigan Street, 14 Sept 2009, *Carolina Vegetation Survey* (NCU).

+$ *Dichanthelium neuranthum* (Griseb.) LeBlond. First known collection: interdune swale N of Avon, 5 Jun 2003, *Carolina Vegetation Survey* (NCU). There are six current populations in Dare County, all from Maritime Wet Grasslands on Hatteras Island (NCNHP database); e.g., swale by Billy Mitchell Airfield, 16 Aug 2012, *Sorrie 13076* (CAHA, NCU).

+ *Eragrostis mexicana* (Hornem.) Link var. *mexicana*. South Nags Head near milepost 18, between highway and beach, single large clump, 10 Jul 1989, *Ludwig 1018* (NCU). This collection is the first for North Carolina for this alien.

+ *Eragrostis secundiflora* J. Presl subsp. *oxylepis* (Torrey) S.D. Koch. Locally common in disturbed sandy roadsides at former Little Kinnakeet Coast Guard Station, Hatteras Island, 18 Sep 2012, *Sorrie 13099* (CAHA, NCSC, NCU). It is considered to be alien in North Carolina.

+* *Eremochloa ophiuroides* (Munro) Hackel. The first report from Dare County is from the 1990s at Jockey's Ridge State Park (JRSP plant list). Today it is common along US 64, NC 12, and NC 158 in Dare and Tyrrell counties (*Sorrie 13229* NCU; *13259* CAHA, NCU).

* *Festuca subverticillata* (Pers.) Alexeev. First known collection: Dare, abandoned home, Wanchese, 31 May 1959, *Crutchfield 3642* (NCU). Discovered new to Tyrrell at Pettigrew State Park in a Natural Lake Shoreline Swamp, 28 May 2013, *Sorrie 13168* (NCU).

+ *Heteropogon melanocarpus* (Ell.) Ell. ex Benth. First known collection: Roanoke Island, 16 Oct 1950, *Schallert 3752* (NCU). Radford, Ahles, and Bell (1968) recorded it from New Hanover County, North Carolina, and 3 counties from southern South Carolina. The Dare County specimen has no habitat data but is almost certainly adventive.

+* *Hymenachne hemitomon* (J.A. Schult.) C.C. Hsu [formerly *Panicum hemitomon*]. In Dare County, this grass forms remarkable floating mats along Milltail Creek, anchored to soil only at the shoreward side, the culms intertwined and forming mats up to 5 m wide x 50 m long, 29 May 2013, *Sorrie 13173* (GH, NCSC, NCU, US). In Tyrrell County it is occasional at the edge of a Floating Bog along New Lake Fork of Alligator River.

+*$ *Luziola fluitans* (Michx.) Terrell & H. Robinson. Locally abundant in roadside ditches along NC 94 in Tyrrell County, 13 Aug 2012, *Sorrie 13066* (NCSC, NCU); also in similar ditches along US 264 in Dare County (NCNHP database).

+* *Microstegium vimineum* (Trin.) A. Camus. First known specimen: Nags Head Woods, 1991, *Stalter 61* (CAHA 2064). More recent specimens were collected there by Krings (cited in Krings 2010). It is locally common in moist soil bordering Interdune Marshes and Interdune Ponds at Nags Head Woods, Kitty Hawk Woods, and Buxton Woods; also in a Natural Lake Shoreline Swamp at Pettigrew State Park in Tyrrell County.

$ *Oplismenus hirtellus* (L.) Beauv. subsp. *setarius* (Lam.) Mez ex Ekman. Mapped for Dare County by Blomquist (1948) and Radford, Ahles, and Bell (1968). First known specimen: sands at Cape Hatteras, 21 Oct 1955 *Radford and Browne, Jr. 8783* (NCU). It is locally common in Maritime Evergreen Forest, Buxton Woods, 20 Sep 2012, *Sorrie 13111* (CAHA, NCSC, NCU). This represents its northern range limit.

+* *Panicum virgatum* L. var. *spissum* Linder. This variety was not recognized by Radford, Ahles, and Bell (1968). First known collections: Dare County, landward side of Hatteras Island near Pea Island, 7 Aug 1954, *Silliman and Munson s.n.* (NCU); Tyrrell County, ditch near NC 94 and Alligator River, 6 mi N of Kilkenny, 6 Aug 1958, *Radford 39225* (NCU). In North Carolina these plants inhabit brackish marshes and their edges, have caudex-like rhizomes, spikelets range from 3.6-4.0 mm, first glumes range from 2.4-3.0 mm, and spikelets have longer, more attenuated tips than those of var. *cubense* Griseb. Thus, they match plants of var. *spissum* as described by Linder (1922) and match specimens from Maryland northward. Var. *cubense* is commonly found across the Coastal Plain in fresh water seepage slopes and wet pine savannas, disjunct to montane seepage bogs. The nominate variety is known in the state only from a few scattered collections from highly disturbed habitats and may not be native in North Carolina. Heretofore, var. *spissum* was documented to occur south to Delaware and Maryland (Weakley 2012). Recent collections include: Dare County, common on low dike through brackish marsh, Point Peter Road, 12 Jul 2012, *Sorrie 13143* (NCU); Tyrrell County, common at roadside edge of brackish marsh, Alligator River at NC 94, 14 Aug 2012, *Sorrie 13068* (NCU).

Paspalum praecox Walt. First known collection: not available at this time; NCU specimens are currently on loan. It was mapped in Dare and Tyrrell counties by Blomquist (1948), but only Dare County by Radford, Ahles, and Bell (1968). It is uncommon at a roadside moist with seepage, N of Wanchese, Roanoke Island, 8 Oct 2013, *Sorrie 13269* (NCSC).

+$ *Paspalum vaginatum* Swartz. Mapped as far north as Hyde County by Blomquist (1948) and Radford, Ahles, and Bell (1968). It was collected in Dare County from a Maritime Wet Grassland near Cape Hatteras Point campground, 9 Jul 2012, *Sorrie 13025* (CAHA, NCU). This represents a new northern range limit.

+# *Schizachyrium littorale* (Nash) Bickn. This taxon was synonymized under *Andropogon scoparius* Michx. in Radford, Ahles, and Bell (1968), but its distinctiveness was clarified by Bruner (1987). First known collection: 6 mi N of Whalebone Junction, 19 Sep 1974, *McCaffrey s.n.* (FLAS). Weakley (2012) stated that it is absent from the Outer Banks north of Hyde County, but in fact it is locally dominant on stable and semi-stable dunes at Buxton, Jockey's Ridge State Park, Nags Head Woods, and northward.

Sorghastrum elliottii (Mohr) Nash. First known collection: Buxton Woods, 1940, *Fosberg 17836* (DUKE). It is known only from Maritime Evergreen Forest at Buxton (*Sorrie 13123* CAHA,

NCU) and several places in Maritime Deciduous Forest at Nags Head Woods (*Krings 1210 and 1322* NCSC).

Sphenopholis nitida (Biehler) Scribner. First known collection: maritime forest 1.5 mi N of Kitty Hawk, 22 May 1954, *Radford 8085* (NCU). Recently it was collected from Maritime Deciduous Forests at Nags Head Woods, 19 Apr 2012, *Sorrie 12924* (NCSC, NCU, US) and at Kitty Hawk Woods, 2 May 2013, *Sorrie 13155* (NCU, US).

Sporobolus clandestinus (Biehler) Hitchc. First known collection: maritime forest, Kitty Hawk, 8 Oct 1961, *Radford 44486* (NCU). It was rediscovered there on 17 Sep 2013, *Sorrie 13237* (NCSC, NCU), growing in the company of *Sorghastrum elliottii, Tridens chapmanii, T. flavus,* and *Aristida lanosa*.

+ *Stenotaphrum secundatum* (Walt.) Kuntze. Locally common on the disturbed margin of Old Doctor's Road, Buxton Woods, 12 Jun 2012, *Sorrie 13001* (CAHA, NCU). While perhaps native in southeastern North Carolina and southward (Weakley 2012), the Dare County population is undoubtedly adventive.

+$ *Tridens chapmanii* (Small) Chase. First known collection: maritime forest at Duck, 21 Oct 1955, *Radford 8772* (NCU); specimen originally determined as *T. flavus*, annotated to *T. chapmanii* by R. LeBlond. It was uncommon at Kitty Hawk Woods, 17 Sep 2013, *Sorrie 13238* (NCU) and along Old Nags Head Woods Road, 31 Oct 2013, *Sorrie 13282* (NCSC, NCU). In North Carolina, these populations are disjunct some 300 km from Bladen County and from the Sandhills of the inner Coastal Plain.

POLYGONACEAE

+ *Persicaria longiseta* (de Bruijn) Kitagawa. First discovered at Dare Bombing Range, wet ditch along Bluewing Road, 1 Nov 2013, *Sorrie 13285* (NCU, NCSC); also seen on moist roadsides of Covered Bridge Road, Kitty Hawk Woods, 31 Oct 2013. This invasive alien was first collected in North Carolina in 1958 in two mountain counties and has now spread across the state.

RANUNCULACEAE

$ *Clematis catesbyana* Pursh. [*C. ligusticifolia* Nutt. ex Torrey & Gray] First known collection: depression between dunes, Duck, 28 Aug 1952, *Radford 6601* (NCU). This species has been known from the Duck area ever since, collected there in a disturbed, wooded roadside, 17 Sep 2012, *Sorrie 13091* (NCSC, NCU). A small population was found in Maritime Evergreen Forest in Buxton, 11 Jun 2012, *Sorrie 12993.1* (NCU).

ROSACEAE

Amelanchier canadensis (L.) Medik. Examination of specimens and additional field work by Krings (2010) confirm that all Outer Banks records of *A. arborea* (Michx. f.) Fern. and *A. obovalis* (Michx.) Ashe actually are *A. canadensis*. First known collection: Roanoke Island, shore of Albemarle Sound S of ferry landing, 18 Mar 1938, *Totten s.n.* (NCU). Plants are uncommon and sporadic in Maritime Forests at Nags Head Woods, Kitty Hawk Woods, and Buxton Woods (specimens cited by Krings 2010 and Clark et al. in press).

RUBIACEAE

+ *Galium orizabense* Hemsl. subsp. *laevicaule* (Weatherby & S.F. Blake) Dempster. Discovered in Maritime Evergreen Forest at Buxton, 11 Jun 2012, *Sorrie 12992* (NCU). A few other populations have been found along the main east-west ridge through Buxton Woods. These are the

northernmost extant populations; historically it was collected from Pasquotank County, North Carolina, and Brunswick County, Virginia (Weakley, Ludwig, and Townsend 2012).

+ *Galium uniflorum* Michx. Scattered in Maritime Deciduous Forest and Maritime Evergreen Forest from Buxton N to Kitty Hawk Woods. Collections include Nags Head Woods, 1 May 2013, *Sorrie 13148* (NCU) and Buxton Woods, 15 May 2012, *Sorrie 12953* (NCU).

SALICACEAE

+* *Populus heterophylla* L. Two trees were found in a small swamp along Covered Bridge Road, Kitty Hawk Woods, 31 Oct 2013, *Sorrie 13280* (NCU, NCSC). This is the sole Dare County and Outer Banks record. It also was seen in Nonriverine Wet Hardwood Forest in Tyrrell County at the Washington County line, 18 May 2012.

SMILACACEAE

+ *Smilax bona-nox* L. var. *littoralis* Coker ex Sorrie. This taxon was not included at any rank in Radford, Ahles, and Bell (1968). First known collection: sand dunes near Fort Raleigh, Roanoke Island, 3 Aug 1937, *Totten s.n.* (NCU). Coker (1944), in a study of woody *Smilax*, described var. *littoralis* as lacking spines on tubers and runners, aerial canes lacking scurfy surface trichomes, and inhabiting coastal dunes and scrub. In contrast, *S. bona-nox* var. *bona-nox* possesses spines on tubers and runners, has abundant whitish scurfy trichomes on aerial canes, and occurs inland in riverine floodplain forests. Specimens at NCU confirm var. *littoralis* from Brunswick, Pender, Carteret, Pamlico, Hyde, Dare, and Currituck counties, North Carolina (Sorrie 2014c). A collection from Northampton County, Virginia may be this variety: end of County Rd 662 on Ramshorn Bay, 5 Mar 1966, *James 3755* (NCU); it would represent the northernmost range limit. Var. *littoralis* is common in moist to xeric maritime sands in Dune Grass, Stable Dune Barren, Maritime Shrub, and Maritime Evergreen Forest communities throughout the Outer Banks of Dare County and also locally on Roanoke Island.

XYRIDACEAE

+ *Xyris ambigua* Beyr. ex Kunth. This yellow-eyed-grass was first reported from Dare County at Jockey's Ridge State Park (park plant list) and found to be numerous in moist grassy Interdune marshes at the bases of high dunes, 30 Oct 2013, *Sorrie 13277* (NCU). It was also collected from a wet roadside slope and ditch, NC 345, N of Wanchese, Roanoke Island, 18 Sep 2013, *Sorrie 13249* (NCU).

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TECHNIQUES FOR IMPROVING THE QUALITY AND QUANTITY OF DNA EXTRACTED FROM HERBARIUM SPECIMENS

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ABSTRACT

There is a need to modify DNA extraction methods to obtain amplifiable DNA from herbarium specimens that are relatively old — we explored several methods to improve both quality and quantity of DNA obtained from a range of specimens of Asteraceae. Leaf tissue was sampled from herbarium specimens of varying ages. Modifications were made to the Qiagen DNeasy® Plant Mini Kit and the CTAB Extraction protocols. Comparison of the results of both protocols for recently collected and older specimens demonstrated that better quality and greater quantity of DNA was obtained with the modified DNeasy® protocol. The modified DNeasy® protocol was more consistent in yielding amplifiable DNA from herbarium specimens older than 20 years. Modification and optimization of two currently used DNA extraction protocols were successful in yielding quality amplifiable DNA from herbarium specimens of Asteraceae, tribe Astereae, that were up to 127 years old. The concentration and quality of DNA was comparable to that obtained from specimens less than 20 years old.

The use of natural history resources in phylogenetics, biogeography, and population biology, among other areas of biodiversity research, justifies investments in their security and accessibility by federal, state, and private funding agencies. Among the collections supported by these agencies are herbaria, repositories of millions of plant specimens, representing documented snapshots of plant diversity and distribution in space and time. Many have called for increased use of natural history resources for research into species discovery. It is proposed that large numbers of unknown and/or undescribed species are part of these collections (Bebber et al. 2010). In addition to prospects of new species discovery, it is argued that these resources should be utilized in molecular-based studies, justifying financial and time investments in them (Drábková et al. 2002), while protecting wild populations from further degradation. However, while many institutions house valuable plant resources, seldom are researchers able to utilize older plant specimens for molecular investigation. A major obstacle is the securing of high quality, amplifiable DNA from older herbarium specimens (Telle & Thines 2008). Molecular studies, particularly among taxa of Asteraceae – the largest family of flowering plants – can benefit from the use of herbarium resources specifically in cases where taxa are rare or their distribution remote. Also, use of these resources supports current and future investments in them and contributes to the conservation and protection of wild populations. However, despite the abundance of resources in plant collections, researchers are usually restricted to using more recently collected specimens, those collected within the last 20 years. For older specimens, the limiting factor is obtaining high quality, amplifiable DNA.

The problems encountered when using older herbarium specimens for molecular studies stem primarily from specimen collection and processing practices. Post collection processing of specimens, including alcohol treatment, time between collection and drying, and method of drying can have adverse effects on the quantity and quality of DNA obtained (Staats et al. 2011). In addition, the age of the specimens (time since collection) may impede DNA retrieval due to natural DNA degradation over time (Staats et al. 2011). This combination of natural DNA degradation and post collection processing practices that accelerate DNA degradation compounds the problem encountered

when older plant specimens are used. Damaged or degraded DNA hinders PCR-based molecular studies and next-generation sequencing (Lindahl 1993). Obtaining quality DNA from old herbarium specimens usually require several modifications to commonly used protocols (Drábková et al. 2002 and citations therein). Drábková et al. (2002) recommended the use of Qiagen DNeasy® Plant Kit or the extraction methods from Doyle and Doyle (1987, 1990) as the most satisfactory extraction methods, albeit for specimens of graminoids only. The resulting extracts from these protocols must also be purified before they are used as PCR template. These extracts did not, however, consistently produce amplicons that were larger than 350 bp. Because DNA extraction requires the destructive sampling of preserved plant specimens, it is imperative that the extraction techniques employed result in high quality amplifiable DNA, reducing the frequency of sample removal from specimens, thus preserving the specimens for posterity. In addition to the challenges outlined above, products of plant secondary chemistry, concentrated by the drying of plant tissues, may have a greater impact on the quality of DNA recovered from older herbarium specimens. These secondary compounds can impede downstream use of extracted DNA as they inhibit reactions and processes in which the DNA extract is utilized.

Here we address some of the issues associated with obtaining high quality, amplifiable DNA from older herbarium specimens of Asteraceae taxa. We discuss modifications to two commonly used extraction protocols and their utility among herbarium specimens of varying ages. The modifications employed are relatively cheap and easy to implement, without substantial increases in processing time. Specifically, we utilized strategies to increase the concentration of DNA while reducing the levels of impurities in the DNA extracted from herbarium specimens that are older than 20 years.

Materials and methods

Plant samples for this study were obtained from herbarium specimens. Sampled taxa included species from Asteraceae, tribe Astereae (Appendix 1). The collection year of specimens ranged from 2013 to 1887, 0–127 years old (at the time of this study). Two methods of DNA extraction were explored and modified several times to optimize for DNA quantity and quality. Samples of desiccated leaves collected close to the apex of specimens were stored in silica gel prior to DNA extraction. For both methods of extraction, 20-40 mg of leaf tissue was pulverized with a Mini-Beadbeater-8 (Bio Spec Products Inc. Bartlesville, OK).

Optimization of the hexadecyltrimethylammonium bromide (CTAB) method (modified from Doyle and Doyle 1987 & 1990) involved reduction of the volume of all reagents to facilitate the use of micro-centrifuge tubes, a useful though not novel strategy. To the pulverized tissue, 600 µL of 2X CTAB and 20mg polyvinyl polypyrolidone (PVP) were added and mixed by vortexing. The samples were incubated for 1 hr 30 min at 70°C, ensuring a more thorough lysis of cells to increase quantity of DNA obtained from the tissue. Following incubation, 600 µL chloroform:isoamyl alcohol (24:1) was added to the samples and mixed. Samples were centrifuged for 20 min at 13,000 RPM. The top aqueous phase was collected for DNA isolation while discarding pellets with cellular debris. In order to degrade RNA, 2 µL of RNaseA (New England BioLabs Inc., Ipswich, MA) was added to samples and incubated for 30 min at 37°C. DNA from samples was precipitated with 540 µL of isopropanol (-20°C), incubated for 15 min at 25°C, then centrifuged for 4 min at 13,000 RPM. Pelleted DNA was washed with 500 µL of 75% ethanol, centrifuged for 4 min at 13,000 RPM and dried for 5 min in a Savant SpeedVac® (Thermo Fisher Scientific Inc., Maddison, WI). Dried pellets were resuspended in 80 µL 1X TE buffer (10mM Tris pH 7.4, 1mM EDTA). To this, 8 µL of 7.5M ammonium acetate and 180 µL of 100% ethanol were added and mixed. This mixture was incubated for 30 min at 25°C then centrifuged for 4 min at 13,000 RPM. Pellets were isolated and washed with 500 µL of 75% ethanol, centrifuged for 4 min at 13,000 RPM, then dried in a SpeedVac® for 5 min. The pelleted-DNA was resuspended in 100 µL 1X TE and stored at -20°C.

DNA was also extracted from pulverized leaf tissue using the Qiagen DNeasy® Plant Mini Kit and protocol. The protocol was modified and optimized for extraction of DNA from recently collected and ancient herbarium specimens. Pulverized tissue was mixed with 450 µL of Buffer AP1, 4 µL of RNaseA and mixed vigorously by vortexing. The mixture was then incubated for 60 min at 70°C to lyse the cells. After lysing, 130 µL of Buffer AP2 was added and the lysate incubated for 60 min at 4°C to precipitate detergent, proteins and polysaccharides. After this precipitation step, the DNeasy® protocol was followed as prescribed by the manufacturer until the DNA elution step. To elute the DNA 50 µL of Buffer AE was added to the spin column followed by an extended incubation time of 10 min, instead of the recommended 5 min. This step was repeated to reach final volume of 100µL.

DNA quality and concentration were evaluated using a NanoDrop Lite (NanoDrop Products, Wilmington, Delaware). We recorded A260/A280 ratios as indicative of DNA purity (1.7-1.9 indicating pure DNA) and the concentration of DNA in each sample. Extracted DNA samples were stored as stock solutions at -20°C. Subsequently, working solutions were prepared through serial dilutions for use as template in polymerase chain reactions (PCR). PCR utilized nuclear ribosomal DNA (nrDNA), spanning external transcribed spacer (*ETS*) and internal transcribed spacer (*ITS*) and chloroplast DNA, spanning *psbA-trnH* and *ycf1 3300-4280* for amplification of DNA. In order to access the effectiveness of these extracts in amplifying DNA we used regions of variable lengths, 350-550 bp in *ETS*, 600-900 bp in *ITS*, 250-400 bp in *psbA-trnH* and 700-1000 bp in *ycf1 3300-4280*.

Results and Discussion

Extracts obtained using the unmodified CTAB protocol produced high concentrations of DNA, on average 234 ng/µL (mean A260/A280 ratio = 1.63). However, we were unable to obtain amplicons with these extracts when used as PCR template. The same taxa were sampled using the unmodified DNeasy® protocol, which produced on average 92.5 ng/µL (mean A260/A280 ratio = 1.24). These extracts also failed to produce amplicons for most DNA regions tested. Extracts obtained from modifications to the CTAB protocol displayed 519.8 ng/µL mean DNA concentration and mean A260/A280 ratio of 1.32. When the samples were subjected to the modified DNeasy® protocol the DNA concentration of the extracts was on average 87.9 ng/µL (mean A260/A280 ratio = 1.38). Comparisons of extracts obtained from the modified DNeasy® and CTAB protocols showed that extracts obtained from the modified DNeasy® protocol were more consistent in amplicon production when used as PCR template. This was the case despite the tendency of the modified CTAB protocol to yield higher concentrations of DNA compared to the modified DNeasy® protocol. As a result, we continued to refine and optimize the DNeasy® protocol for extraction of DNA from older herbarium specimens, resulting in amplifiable DNA from specimens collected 127 years ago (Table 1).

Table 1. DNA quality and quantity using the modified DNeasy® method on recent and old herbarium specimens.

Taxon Name	Year collected	A260/A280	[DNA] (ng/µL)
Chrysopsis mariana	1967	1.65	71.1
Chrysopsis mariana	2008	1.65	79.6
Pityopsis ruthii	1900	1.40	44.8
Pityopsis ruthii	2013	1.46	55.0
Heterotheca viscida	1963	1.48	37.9
Heterotheca viscida	2000	1.44	16.4
Noticastrum marginatum	1977	1.51	9.0
Noticastrum marginatum	2011	1.25	94.6

The optimized DNeasy® protocol consistently resulted in amplifiable DNA in more cases than the CTAB protocol. In particular, regions of chloroplast DNA extracted using the modified DNeasy® protocol could be amplified from specimens that were over 100 years old. We recovered, on average, 60 ng/µL of DNA (mean A260/A280 ratio = 1.54) using the modified DNeasy® protocol (Table 2). The total time required for this method increased to approximately 3 hr compared to the original 1 hr. We recovered an average of 406 ng/µL of DNA (mean A260/A280 ratio = 1.4) using the modified CTAB method, and decreased time required for this protocol from ~8 hr to <4 hr (Table 1). The quality of DNA extracted using the modified DNeasy® protocol were significantly better than those from the modified CTAB extractions ($p=0.048$), where seven of the nine sampled taxa produced DNA of higher purity (Table 2).

Table 2. DNA quality (spectrophotometer A260/A280 where 1.70-1.9 indicates pure DNA) and quantity using a modified CTAB protocol and modified DNeasy® method. Note: [f]Extracts from modified CTAB failed to amplify when used as template in PCR for most genes.

Taxon Name	Year collected	CTAB A260/A280	QIAGEN A260/A280	CTAB [DNA] (ng/µL)	QIAGEN [DNA] (ng/µL)
Chrysopsis mariana[f]	1967	1.50	1.65	417.0	71.1
Chrysopsis gossypina	1974	1.27	1.71	188.5	70.1
Heterotheca oregona	1986	1.43	1.48	466.7	41.3
Croptilon divaricatum	1987	1.42	1.43	133.0	25.3
Tomentaurum niveum	1929	1.57	1.65	702.3	59.0
Tomentaurum niveum[f]	1887	1.30	1.14	414.7	14.8
Heterotheca inuloides[f]	1970	1.35	1.53	470.9	66.8
Bigelowia nudata	2000	1.19	1.56	161.1	47.5
Euthamia graminifolia	2001	1.58	1.73	705.1	150.1

The potential benefits of the extracting DNA from old herbarium specimens are great, as this adds to the value of millions of specimens currently housed in natural history collections. We have increased both the quantity and quality of DNA extracted from herbarium specimens of Asteraceae dating up to 127 years old, a large improvement when compared to the oldest specimen, 71 years, in Drábková et al. (2002). We increased DNA concentration using DNeasy® Plant Mini Kit by modifying lysis time for cells, the volume of Buffer AP1 used per reaction, and increased incubation time prior to DNA elution. These modifications also resulted in increased DNA purity (Table 2). Although the overall time required for this protocol has increased, we believe that the yield of amplifiable DNA from relatively old herbarium specimens outweighs the increase in extraction time.

While Drábková et al. (2002) suggested their methods as useful for specimens of graminoids, we have demonstrated a wider application of these extraction methods for specimens of Asteraceae, which have vastly different secondary chemistry and anatomy. We have also reduced the amount of material needed for extractions (between 20-40 mg instead of 100-500 mg). Additionally, DNA extracts from the same specimen or related taxa, ranging from 0 to 127 years old, were used to evaluate the efficacy of the modified and optimized DNeasy® protocol. Interestingly, unlike findings in Drábková et al. (2002), our extracts resulted in successful amplification of DNA from both nuclear and chloroplast regions, ranging from 350 to 1000 bp. These modified protocols were also successful when used for recently collected specimens, increasing the range of specimens that can be harnessed for molecular studies.

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APPENDIX 1. Voucher information for specimens used in this study

Taxon Name	Collector and number	Collection Date	Collection Locality	Herbarium
Bigelowia nudata	Kral 90535	2000	AL: Washington Co.	DOV
Bradburia hirtella	McCrarry 72	1971	TX: Nacogdoches Co.	BALT
Bradburia hirtella	Jones & Jones 455	1987	TX: Brazos Co.	US
Bradburia pilosa	Allen 8361 & Vincent 1685	1978	LA: Union Parish	BALT
Chrysopsis gossypina	Pittillo 2807	1965	GA: Burke Co.	BALT
Chrysopsis gossypina	Rothwell C-60	1974	NC: Jones Co.	BALT
Chrysopsis linearifolia	Davis & Davis 15565	1970	FL: Walton Co.	BALT
Chrysopsis mariana	D'Arcy 2219	1967	FL: Alachua Co.	BALT
Chrysopsis mariana	Strong 3787	2008	FL: Marion Co.	US
Euthamia graminifolia	Naczi 8917	2001	DE: Kent Co.	DOV
Heterotheca inuloides var. *rosei*	Cronquist & Fay 10815	1970	Mexico	US
Heterotheca oregona var. *scaberrima*	Semple & Heard 8588	1986	CA: Santa Clara Co.	BALT
Heterotheca viscida	Bennett 8306	1963	NM: Santa Fe Co.	US
Heterotheca viscida	Carr & Karges 19141	2000	TX: Jeff Davis Co.	TEX/LL
Noticastrum marginatum	Norrbom et al. 11-PE-17	2011	Peru	US
Noticastrum marginatum	Olsen & Escobar 576	1977	Colombia	TEX/LL
Pityopsis ruthii	Ruth 1501	1900	TN: Hiawassee Valley	US
Pityopsis ruthii	Schilling (Aug. 2013)	2013	TN: Polk Co.	TENN
Tomentaurum niveum	Mexia 2598	1929	Mexico	US
Tomentaurum niveum	Pringle s.n.	1887	Mexico	US

APPENDIX 2. CTAB extraction protocol

Sample Preparation

- Prepare 2ml tubes for tissue homogenizer with labels and white zirconia/silica beads
- Warm 2X CTAB to 60°C in water bath
- Homogenize samples in Mini Bead Beater 8 for 2min
- Spin for 1min at 13,000 RPM
- Under the hood
    - Add 600µl 2X CTAB to homogenized sample
    - Add small volume of PVP with sterilized spatula
- Vortex samples; invert and vortex again

Extraction and Isolation of DNA

- Incubate for 1hr 30min at 70°C.
    - Mix manually (DO NOT VORTEX) every 30min
- Add 600µl 24:1 chloroform: isoamyl alcohol to sample
    - Manually mix samples
- Spin for 20min at 13,000 RPM
    - Check for clear liquid and spin again if necessary
- Under the hood
    - Transfer top aqueous phase only to a new 1.5ml microfuge tube

DNA Precipitation

- Add 2µL of RNaseA and incubate 30min at 37°C
- Add 540µl cold isopropanol (-20°C)
    - Mix manually
- Incubate for 15min at 25°C
- Spin samples for 4min at 13,000 RPM
    - Decant supernatant (DNA is present in the pellet)
- Wash pellet with 500µl 75% EtOH and invert tubes or flick w/ finger several times
- Spin samples for 4min at 13,000 RPM
    - Decant supernatant and dry excess liquid by blotting with Kimwipe

- Dry with SpeedVac for 5min

Final Cleaning and Re-Suspension of DNA

- Resuspend pellet in 80µl 1X TE; break up pellet completely
- Add 8µl of 7.5M ammonium acetate, and 180µl of 100% EtOH
- Mix manually and incubate for 30min at 25°C
- Spin for 4min at 13,000 RPM, decant supernatant
- Add final wash of 500µl 75% EtOH, gently invert tubes
- Spin 4min at 13,000 RPM
    - Decant supernatant and dry excess liquid by blotting with Kimwipe
- Dry with SpeedVac for 5min
- Resuspend pelleted DNA with 100µL 1X TE and store at -20°C

APPENDIX 3. QIAGEN DNeasy® Plant Kit Protocol

- Disrupt samples (20-40mg desiccated plant tissue) using Mini Beadbeater-8
    - Centrifuge samples @ 14,000 RPM for 1 min
- Add 450µL Buffer AP1 and 4µL RNase A
    - Vortex samples to thoroughly mix
    - Incubate at 70°C for 60 min
    - Transfer to NEW 2mL microfuge tube
- Add 130µL Buffer P3
    - Mix by inversion
    - Incubate in ice for 60 min
- Centrifuge the lysate @ 14,000 RPM for 5 min
- Pipet clear lysate into a QIAshredder spin column (lilac) placed in a 2mL collection tube
    - Centrifuge @ 14,000 RPM for 2 min
    - Transfer the flow-through fraction (measure volume) into NEW 1.5mL microfuge tube without disturbing the cell-debris pellet
- Add 1.5 volumes of Buffer AW1. MIX IMMEDIATELY

- Pipet 650µL of the mixture into DNeasy® Mini spin column (white) placed in a 2mL collection tube
    - Centrifuge @ 8,000 RPM for 1 min
    - Discard flow-through. Blot-dry the collection tube and reuse
- Repeat step 7 with remaining sample
    - Centrifuge @ 8,000 RPM for 1 min
    - Discard flow-through and collection tube
    - Place DNeasy® Mini spin column into NEW 2mL collection tube
- Add 500µL Buffer AW2
    - Centrifuge @ 8,000 RPM for 1 min
    - Discard flow-through. Blot-dry the collection tube and reuse
- Add 500µL Buffer AW2
    - Centrifuge @ 14,000 RPM for 2 min
- Remove the spin column from collection tube carefully so that the column does not come into contact with the flow-through
    - Discard flow-through and collection tube
- Transfer the spin column to a new 1.5mL microfuge tube
- Add 50µL Buffer AE for elution
    - Incubate at room temperature for 10 min
    - Centrifuge @ 8,000 RPM for 1 min
- Repeat previous step.
- Store in -20°C

Singhurst, J.R. and W.C. Holmes. 2014. Rediscovery of *Selenia aurea* (Brassicaceae) in Texas. Phytoneuron 2014-49: 1–3. Published 20 May 2014. ISSN 2153 733X

REDISCOVERY OF *SELENIA AUREA* (BRASSICACEAE) IN TEXAS

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ABSTRACT

Selenia aurea has been rediscovered in Texas, now known from a population in Fannin County, close to the Oklahoma border. The only other known collection of the species in the state was made in about 1832 by M.C. Leavenworth at Ayish Bayou Settlement (now San Augustine), San Augustine County, about 181 miles (292 km) south southeast of the Fannin County plants. The Fannin County plants grow in a seasonally wet, vernal pool along a limestone ridge.

In 2012, an account was published documenting the historical occurrence of *Selenia aurea* Nutt. (Brassicaceae) in Texas (Holmes et al. 2012). The only previously known record of the plant in Texas was a collection made at Ayish Bayou Settlement (now San Augustine), San Augustine County, in about 1832 by Melines C. Leavenworth. The manuscript ended with the following:

> "Comments on the possibility of rediscovery of the species in Texas are appropriate. In short, this is highly unlikely, largely because of habitat loss, the rock outcrops/glades of this part of Texas [glauconite glades of the Weches Formation in deep east-central Texas] have been mined for rock used on local roads. Those remaining intact are in less than pristine condition, largely due to invasion by non-native woody plants such as *Rosa bracteata* (Rosaceae), *Ligustrum sinense* (Oleaceae), and *Lonicera japonica* (Caprifoliaceae) or are privately held, thus have limited or no access. However, the hope remains that the species may still be found in the state, probably in northeast Texas."

Northeast Texas was considered the most promising region for the species because of its known distribution in adjacent Oklahoma (McCurtain, Choctaw, Pushmataha, Atoka, Johnston, and Carter counties; BONAP 2014) and the presence of suitable habitat (limestone glades) in that part of Texas. Specifically, this includes the counties bordering the Red River (Cooke, Grayson, Fannin, Lamar cos., and a limited portion of Red River Co. near White Rock Community). The distribution of the species (BONAP 2014) includes southwest Missouri, southeast Kansas, Arkansas (Ozark Plateau, Arkansas Valley, and Ouachita Mountains), east Oklahoma, and, as included in this paper, northeast Texas.

Since 2012, several trips have been made in Texas, in conjunction with searches for other plants, in an attempt to relocate the *Selenia aurea* in the deep east-central and northeast regions of the state. These searches were unsuccessful.

In recent (2014) processing of collections from northeast Texas made by the senior author in 2001, several specimens of *Selenia aurea*, unbeknown to us, were discovered among them. Unfortunately, in 2001 the collector was unfamiliar with the species and, along with the junior author,

involved with pursuing other plants. Nonetheless, we are pleased to report the rediscovery of the species in the state. While relocation of the species in Texas is a major accomplishment, it is doubtful that this will appreciably alter the conservation status of the species. It does, however, yield information that may encourage further search for the species.

Figure 1. *Selenia aurea* from Limestone County (*Singhurst & White 10322*). Photo by Darrell Vodopich.

Voucher: **Texas**. Fannin Co.: Randolph Hills, [3.73 mi (6.01 km) SSW (168°) of Randolph], ca. 0.3 mi S of jct of Co. Rd. 4715 and Co. Rd. 4720 on Co. Rd. 4715, N side of Co. Rd. 4714, seasonally wet, vernal pool along ridge top, area of Austin Chalk prairie and glades, 6 Apr 2001, *J. Singhurst and M. White 10332* (BAYLU). Figure 1.

The *Selenia aurea* site in Fannin County is located on a ridge top that is part of the Randolph Hills, a series of hills south of Randolph, Texas. The ridge top consists of Austin Chalk limestone — the vegetation along the ridge includes Blackland Prairie, limestone glades, and hardwood slope forest. The prairie portion is characterized by *Schizachyrium scoparium*, *Bouteloua curtipendula*, and *Sporobolus compositus*. The glades are dominated by *Juniperus ashei*, *Ceanothus herbacea*, *Rhus trilobata*, *Cercis canadensis* var. *texensis*, *Lonicera sempervirens*, *Baptisia australis*, *Echinacea angustifolia*, *Marshallia caespitosa*, *Penstemon cobaea*, *Hedeoma reverchonii*, *Paronychia virginica*, *Astragalus nuttallianus*, *Stenaria nigricans*, *Thelesperma filifolium*, *Galium virgatum*, *Solidago* spp., *Brickellia eupatorioides*, *Scutellaria drummondii*, *Allium drummondii*, *Sisyrinchium* sp., *Physaria gracilis*, *Draba cuneifolia*, and *Bouteloua rigidiseta*. The hardwood slope forest is dominated by *Quercus buckleyi*, *Ulmus crassifolia*, *Sideroxylon lanuginosa*, *Viburnum rufidulum*, *Cornus drummondii*, *Forestiera pubescens*, *Cocculus carolinus*, and *Smilax bona-nox*. The forest understory includes *Carex planostachys*, *Dichanthelium* sp., *Geum canadense*, and a small patch of *Orobanche uniflora*.

The population of *Selenia aurea* consisted of slightly less than 50 plants in about a two meter square, seasonally wet, vernal pool (within a glade along the ridge) containing thinly developed clay sediments, various mosses, and *Nostoc* sp. (Nostocaceae). All plants in the population were in fruit.

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HYMENACHNE AMPLEXICAULIS NEW FOR LOUISIANA

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ABSTRACT

Hymenachne amplexicaulis, West Indian marsh grass, is reported new to Louisiana. In the continental United States this pantropical, wetland species was previously known only from Florida. The species is a forage plant in wet, tropical areas but has become an unwanted pest, replacing native plants where recently introduced.

An unknown grass, brought to attention by JKS, was first noticed by a rice farmer growing as several sporadic clumps along the banks of a canal that served the irrigation needs for rice production near the community of Gueydan, Vermilion Parish, Louisiana. Specimens were collected by Doug Leonards and pressed, dried, and delivered to the LSU Herbarium for identification.

The initial identification of *Hymenachne amplexicaulis* (Rudge) Nees was made using the interactive key by Watson and Dallwitz (1992). Comparisons with published descriptions and with authentic material from various on-line sources all supported that determination (Wunderlin & Hansen 2008; Center for Aquatic and Invasive Plants 2014). The species name is based on *Panicum amplexicaule* and the type specimen also compares favorably with the unknown, BM 000938735 "ex. herb Rudge" (JSTOR Global Plants Initiative 2014).

Voucher specimen. **Louisiana**. Vermilion Par.: ca. 0.4 mi S of La. Hwy 14 and ca. 0.34 mi E of Alvie Rd. or ca. 2 mi WSW of the community of Gueydan, sporadic clumps on canal banks near inlet of rice irrigation pump with other clumps nearby, 30.01487° N, 92.54222° W, ca. 1 m elevation, 27 Nov 2013, *Leonards s.n.* (LSU 135072)

The geographic range for *Hymenachne amplexicaulis* includes west tropical Africa, Australia, the Caribbean, China, India, Malesia, Mexico, Papuasia, and South America (Clayton et al. 2006). Prior to this report West Indian marsh grass was known in the USA from the southern half of peninsular Florida and Leon county in northern Florida (Wunderlin & Hansen 2008; Robert K. Godfrey Herbarium 2014; USDA, NRCS 2014.). Leon County, approximately 500 miles to the east, is the documented location nearest the Vermilion Parish site.

Opinions apparently differ on whether the taxon is native to the USA. Barkworth (2003) noted that it is native to Florida. The U.S. National Park Service (2009) indicates it was first reported in a ponded pasture in Palm Beach County, Florida, more than 30 years ago. Whether this was the result of natural or intentional introduction could not be determined. The species is grown as cattle forage in wet, tropical areas and could have been planted in Florida for that purpose.

Fig. 1. *Hymenachne amplexicaulis* specimen collected in Vermilion Parish, Louisiana

Fig. 2. *Hymenachne amplexicaulis* morphology. Left: spikelets, primary glume and sterile lemma evident in image on the left, base of primary glume and secondary glume shown on the right. Right: transverse section of culm internode filled with aerenchymatous tissue.

The mode of introduction of *Hymenachne amplexicaulis* to Louisiana is unknown and thus highly speculative. Seeds or vegetative means from node-bearing stem fragments can accomplish propagation of this species. Southern Louisiana is a potential stop along the Mississippi flyway, a major route for migrating tropical birds (Birdnature 1988) and seed transport from Florida, Mexico, or South America is a likely scenario. The movement of vegetative fragments by agricultural equipment, boats, or by water is another possibility. Water can flow through breaches in the Intracoastal Waterway into irrigation canals in southern Louisiana. However, plant fragments traveling through the Intracoastal Waterway from Florida, Mexico, or elsewhere most likely would encounter seawater and the salt tolerance of *H. amplexicaulis* is unknown.

In Florida *Hymenachne amplexicaulis* is regarded as an ecological threat because it displaces native maidencane (*Panicum hemitomon*) communities and invades various freshwater wetlands such as streams, cypress swamps, and marshes. It colonizes or invades disturbed, wet sites including drainage canals and pastures. Plants can also grow as flotant in open water. In nutrient rich wetlands, mature plants form extensive colonies by producing stolons that extend many feet underwater (Center for Aquatic and Invasive Plants 2014, U.S. National Park Service 2009).

Except for last year, southern Louisiana has experienced a series of mild winters that may have allowed *Hymenachne amplexicaulis* to become established. Observations will be made at the Vermilion Parish site to determine whether this species survived the recent winter, suggesting that it is sufficiently cold tolerant to persist in the central Gulf region thus giving it the potential to become a pest.

In coastal and central Queensland Australia, the species has become an unwanted pest of stream banks, wetlands, and irrigation ditches. It has also invaded low-lying sugarcane fields, fish habitats, and natural wetlands of high conservation value. It has been declared a "class 2 pest" by the Australian Department of Agriculture, Fisheries and Forestry 2014.

Hymenachne amplexicaulis may be more widely established along the Gulf Coast but overlooked because of its similarity to another panicoid, wetland species, *Sacciolepis striata* (L.) Nash, American cupscale. Field biologists should look critically at *S. striata* when making identifications. Both taxa grow in similar habitats, are strongly rhizomatous, have broad, auriculate leaf blades and elongated, congested panicles. Features characteristic of *H. amplexicaulis* are solid, pithy internodes, symmetrically attached spikelets, and non-saccate, 5-nerved secondary glumes, while in *S. striata* the internodes are hollow, spikelets are asymmetrically attached, and secondary glumes are saccate and 11–12 nerved (Wipff 2003). A herbarium specimen, spikelets, and culm internode cross-section are shown in Figures 1 and 2.

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Pruski, J.F. *Lowryanthus rubens* (Compositae: Athroismeae), a new genus and species from southeastern Madagascar. Phytoneuron 2014-51: 1–11. Published 20 May 2014. ISSN 2153 733X

LOWRYANTHUS RUBENS (COMPOSITAE: ATHROISMEAE), A NEW GENUS AND SPECIES FROM SOUTHEASTERN MADAGASCAR

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ABSTRACT

The new genus and species **Lowryanthus rubens** Pruski (Compositae) from Madagascar is described. By paleate clinanthia, tailed anthers, 2-banded styles branches, and especially by the strange carbonized, obcompressed, geniculate-rostrate cypselae, **Lowryanthus** Pruski is placed in African-centered tribe Athroismeae, which contains only 3 subtribes, 7 genera, and about 60 species. Although the epappose long-ciliate cypselae and open paniculate capitulescence make confident placement of *Lowryanthus* in either subtribe Anisopappinae or Athroisminae difficult, the carbonized obcompressed cypselar character of *Lowryanthus* is used here to place the new genus in Athroisminae. However, the three other genera of Athroisminae are totally different and characterized by glomerate capitulescences and typically white corollas.

Exploration in Madagascar by a team of botanists from the Missouri Botanical Garden has resulted in the discovery of a hitherto unknown, red-flowered, discoid-capitulate Compositae. This striking plant (Fig. 1) was brought to my attention in 2007 by Porter P. (Pete) Lowry II (MO) and is described here as monotypic *Lowryanthus* Pruski and placed in tribe Athroismeae, which is characterized in part by its strange, carbonized, obcompressed, geniculate-rostrate cypselae (Figs. 2, 5D). An early draft of this manuscript was reviewed in 2007 by Henk Beentje (K) and Arne Anderberg (S), but validation of the plant was withheld pending examination of possible newer collections, the existence of which I was alerted to in 2008 by Pete Lowry. In 2013 this second suite of collections, made by J. Rabenantoandroin in 2008, were processed and mounted at MO. These 2008 specimens were seen recently during routine herbarium specimen filing, and their mature, black, carbonized, geniculate-rostrate cypselae confirm this important character as given in original draft description of *Lowryanthus*. I do not anticipate that possible additional collections will change drastically either the description or circumscription of the plant, and it now appears appropriate to validate the new genus and species, apparently endemic to Madagascar.

LOWRYANTHUS RUBENS Pruski, **gen. et sp. nov.** **TYPE: MADAGASCAR. Toliara**. Anosy Région, Bemangidy Forest, ca. 3 km W of Antsotso, along RN 12a, 65 km N of Ft. Dauphin, humid evergreen forest on steep slope, E of Ivohibe peak, 24° 35' 02" S, 47° 12' 44" E, 100–250 m, 7 Feb 2006, *P.P. Lowry II, J. Rabenantoandro, F. Randriatafika, E. Lowry, E. Ramisy, & B. Mara* 6648 (holotype: MO; isotypes: P [photograph: MO], S, TAN). Figs. 1–5.

Plantae herbaceae perennes vel fruticosae 1–4 m altae, caules rubri subtereti hirsutuli, folia simplicia alterna petiolata, lamina oblanceolata vel anguste obovata 5–19(–25) × 2–7.5(–9.5) cm chartacea pinnativenia eglandulosa hirsutula denticulata, trichomatibus patentibus uniseriatas multicellularibus, petiolo 2–3.5(–5) cm longo; capitulescentia terminalis corymbiformis vel paniculata, pedunculis 7–20 mm longis; capitula discoidea paleacea, involucrum turbinatum vel campanulatum 7–9 × 4.5–8.5 mm, phyllaria 5–8 circiter 2-seriata oblanceolata vel obovata 6.5–8 × 2–5.5 mm, chartacea rubra, clinanthium paleaceum, paleae late lanceolatae vel oblanceolatae 7–11 × 1.5–2.5 mm stramineae vel rubrae, flosculi disci 10–15, corolla anguste campanulata quinquelobata 4–5.8 mm longa rubra vel rosea, tubo 1.5–2.1 mm longo glanduloso necnon piloso, glandulis biseriatis brevistipitatis, limbo anguste ampliato, lobis 1.2–1.5

mm longis subsessile-glandulosis, antherae basi caudatae, styli ramuli bilineati 1.2–1.3 mm longi; cypselae obcompressae obovoidae 3.7–5 × usque 2 mm rostratae epapposae longiciliatae.

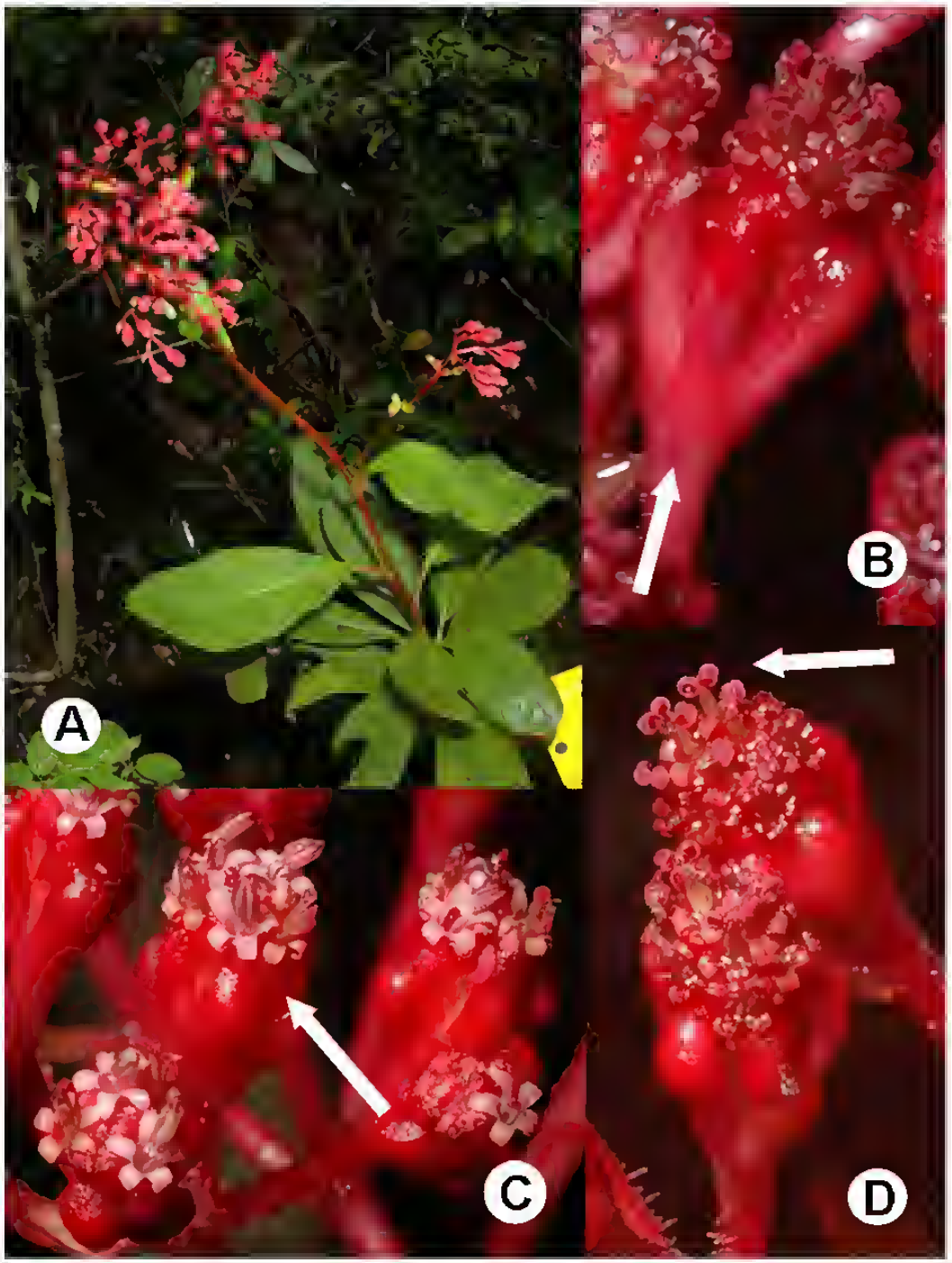

Figure 1. Field photographs of *Lowryanthus rubens*. A. Habit. B. Capitulum showing base of involucre (arrow) and ca. 2-seriate phyllaries. C. Capitula showing reflexed pinkish disk corolla lobes (arrow) and exserted anther cylinders with styles yet to protrude. D. Close up of two capitula showing recurved style branches (arrow) and the patent trichomes of the peduncles. (*Lowry et al. 6648*, photographs by P.P. Lowry II)

Figure 2. SEM micrograph of convex abaxial face of an immature cypsela of *Lowryanthus rubens* showing geniculate rostrum (upper right) (*Antilahimena et al. 4801*, MO; sample preparation method is as given in Pruski 2012).

Perennial herbs to shrubs, 1–4 m tall; stems ascending to erect, few-branched distally, striate, subterete to angled or even somewhat flattened in capitulescence, reddish, slightly hirsutulous distally, leafy in the proximal half with somewhat congested internodes, these becoming well-spaced distally, internodes 1–4(–12) cm long, pith solid. **Leaves** simple, alternate, petiolate; blade progressively reduced in size distally, oblanceolate to narrowly obovate, 5–19(–25) × 2–7.5(–9.5) cm, chartaceous to stiffly so, venation pinnate, secondary veins departing from midrib at angles of 45° or greater, third order venation obscure, surfaces eglandular, hirsutulous, trichomes patent, uniseriate, multicellular, without well-developed subsidiary cells, abaxial surface of immature leaves sometimes densely hirsute, blade base attenuate onto petiole, margins denticulate, the closely spaced callous-tipped teeth usually ca. 0.5 mm long, apex obtuse to rounded; petiole narrowly winged to base, 2–3.5(–5) cm long, canaliculate, rose-colored, broadened basally and subclasping (subamplexicaul) the stem. **Capitulescence** mostly terminal, pluricapitulate, open, corymbiform-paniculate, branching

alternate appearing more or less divaricate, branches reddish, often 1-bracteolate, slightly hirsutulous, bracteoles typically positioned toward proximal half of branch, oblanceolate, 5–8 × 1–2 mm wide; peduncles reddish, somewhat stout, 7–20 mm long, slightly hirsutulous, often 1(–4)-bracteolate, bracteoles resembling those of the capitulescence branches, often positioned (0–)2–4 mm proximal to subtended capitulum. **Capitula** discoid, 10–15-flowered, 10–12 mm tall; involucre turbinate to narrowly campanulate, 7–9 × 4.5–8.5 mm, sometimes appearing double by closely subtending peduncular bracteoles; phyllaries 5–8, oblanceolate to obovate, 6.5–8 × 2–5.5 mm, subequal or slightly graduated, loosely imbricate, ca. 2-seriate, erect, reddish, bracteoles and outer phyllaries not articulated basally, stiffly chartaceous, obscurely ca. 5–7-nerved, glabrous or short-ciliate distally, apex somewhat cucullate especially in bud, disk corollas partly exserted from top of involucre; clinanthium paleate, hemispherical to clavate, 1.5–4.5 × 1–2.5 mm; paleae broadly lanceolate to oblanceolate, 7–11 × 1.5–2.5 mm, nearly planar grading to the inner ones somewhat conduplicate, chartaceous, stramineous with rose-colored apices, 3–5-nerved, glabrous or short-ciliate distally, apically rounded to less commonly truncate. **Ray florets** none. **Marginal pistillate florets** apparently none. **Disk florets** 10–15, bisexual, 5-merous, the outermost sometimes aborted; corolla actinomorphic, narrowly campanulate, 5-lobed, 4–5.8 mm long, tissue moderately thick, tube 1.5–2.1 mm long, reddish with pinkish lobes, broadened basally around nectary, with short-stipitate biseriate-glandular trichomes (similar to those in Eriksson 1995: 118, Fig. 4), also often pilose, the limb moderately ampliate, throat glabrous or stipitate-glandular, lobes 5, 1.2–1.5 mm long, reflexed to slightly so, subsessile-glandular, 2-nerved, nerves intramarginal; filaments 1.2–1.5 mm long, glabrous, collar same diam. as filaments, shorter than the tails, collar cell walls evenly thick, anthers often fully exserted, ca. 2.2 mm long, pinkish, caudate (sterile-tailed) or calcarate-caudate (tails partly polleniferous), thecae ca. 1.5 mm long, endothecial tissue polarized, thecae and connectives somewhat discolorous, tails ca. 0.7 mm long, distal tail surface short-papillose, papillae apices rounded, tails of adjacent thecae appressed to slightly connate, apical anther appendage elliptic-ovate, ca. 0.3 mm long, longer than wide, well-differentiated from thecae, slightly concave longitudinally, non-sculptured; pollen markedly echinate, white; style 4.7–6 mm long, red, exappendiculate, trunk 3.5–4.2 mm long, basally glabrous, non-enlarged, branches 1.2–1.3 mm long, broadly linear, tangentially spreading to recurved, each with a 2-banded stigmatic surface, apically acute to obtuse, with short sweeping papillae, papillae apices rounded, style immersed in basal nectary, nectary ca. 0.6 mm long, commonly positioned asymmetrically atop rostrum. **Cypselae** obcompressed (tangentially flattened), obovate in outline, 3.7–5 × to 2 mm, rostrate, epappose, body and rostrum black-carbonized, eglandular, faces finely roughened, phytomelanin deposits first manifest in spots, glabrous to sparsely pilose distally, abaxial face convex, adaxial face concave, body ultimately with 2 well-developed lateral shoulders, the rostrum thus appearing as arising from a slight recession on the top of the fruit, margins to 0.4 mm broad, sometimes brownish when maturing, spreading-antrorse long-ciliate, trichomes multicellular, biseriate-celled, to ca. 2.5 mm long, falsely resembling pappus (nearly as to position on the technically epappose cypselae), but ontogenetically not homologous and not borne upon the apical annulus, terminal trichome cells erect and non-diverging, rostrum broad, ca. 0.7 mm tall, strongly deflected (geniculate) abaxially, annulus a minute ring atop rostrum; carpopodium nearly annular, ca. 0.3 mm long, somewhat broadly triangular in cross-section, stramineous. **Chromosome number** unknown.

Paratypes. **MADAGASCAR. Toliara.** Bemangidy, Commune Iabakoko, Fokontany Antsontso, Ivohibe forest, 24° 34' 13" S, 47° 12' 01" E, 286 m, 23 May 2006, *Antilahmena et al. 4801* (MO, P, S, TAN, TEF); Anosy, Fort Dauphin, Iabakoho, Antsotso, 24° 34' 15" S, 47° 12' 05" E, 280 m, 2 Apr 2008, *Rabenantoandro et al. 1895* (MO, P, TAN); Anosy, Tolagnaro, Iabakoho, Antsotso avaratra. Forêt dense humide de basse altitude d'Ivohibe. 24° 34' 03" S, 47° 12' 09" E, 270 m, 3 Apr 2008, *Rabenantoandro et al. 1903* (MO, P, TAN); Fort-Dauphin, Iabokoko, Antsotso, Forét Ivohibe, 24° 33' 52" S, 47° 14' 25" E, 112 m, 26 Nov 2005, *Razakamalala et al. 2369* (MO, P, S, TAN).

Figure 3. Holotype of *Lowryanthus rubens* (*Lowry et al. 6648*, MO).

Etymology. I am both pleased and privileged to dedicate this new genus to Porter P. (Pete) Lowry II (MO), director of MBG's Madagascar program and collector of the type material. Pete kindly and enthusiastically showed me photographs of his then-unrecognized, red-flowered Compositae collection and shortly thereafter routed the initial collections from 2005 and 2006 to me for identification. The epithet refers to the crimson-red branchlets, phyllaries, and corollas.

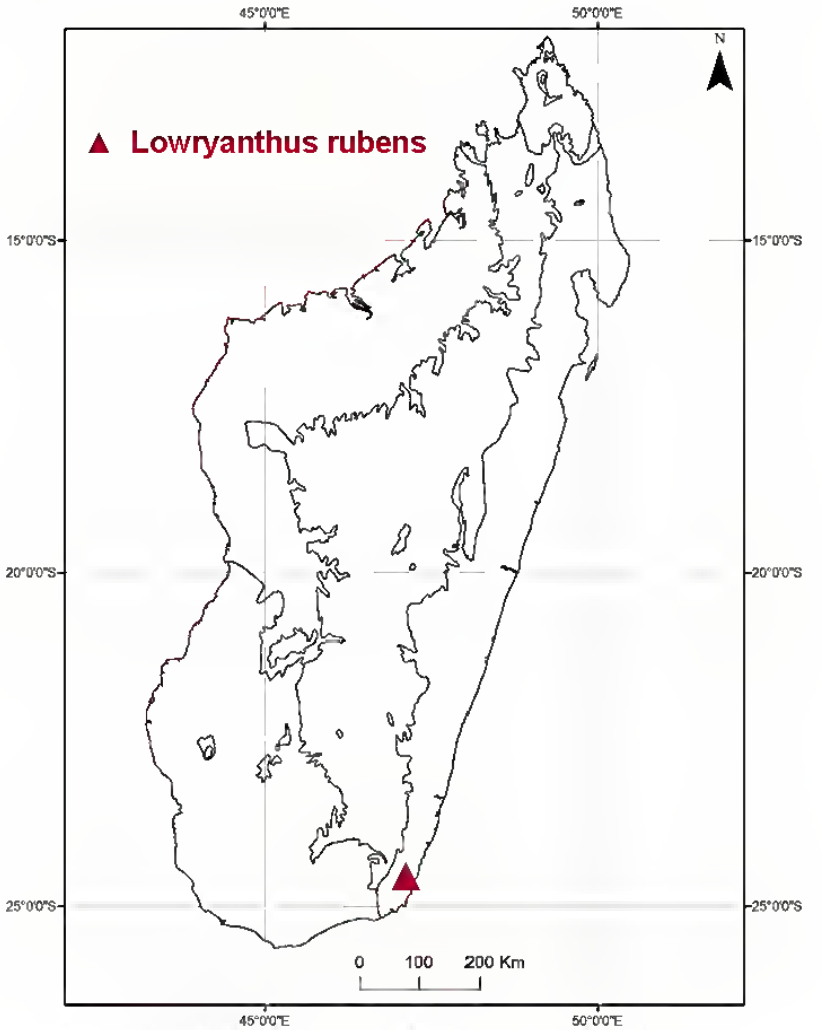

Figure 4. Distribution map (with the five major biozones of Madagascar indicated) of *Lowryanthus rubens*.

Habitat and ecology. *Lowryanthus rubens* is known from only a handful of collections made within a few kilometers of each other in the Bemangidy-Ivohibe forest, downhill from Ivohibe peak and about 50 kilometers north of Fort Dauphin in southeastern Madagascar. *Lowryanthus rubens* occurs between about 100–286 meters elevation in low-elevational humid evergreen forests on the eastern slope of the Tsitongambarika range, the easternmost mountain chain in southern Madagascar and basically bordering the Indian Ocean. The Bemangidy-Ivohibe forest is of special interest as it is among the few remaining regional low-elevational wet forests. The species has been collected in flower from November to May and is pollinated possibly by insects. I do not know the soil type where the plants grow. Five of the seven known genera of Athroismeae occur in Madagascar, but only *Lowryanthus* is endemic there.

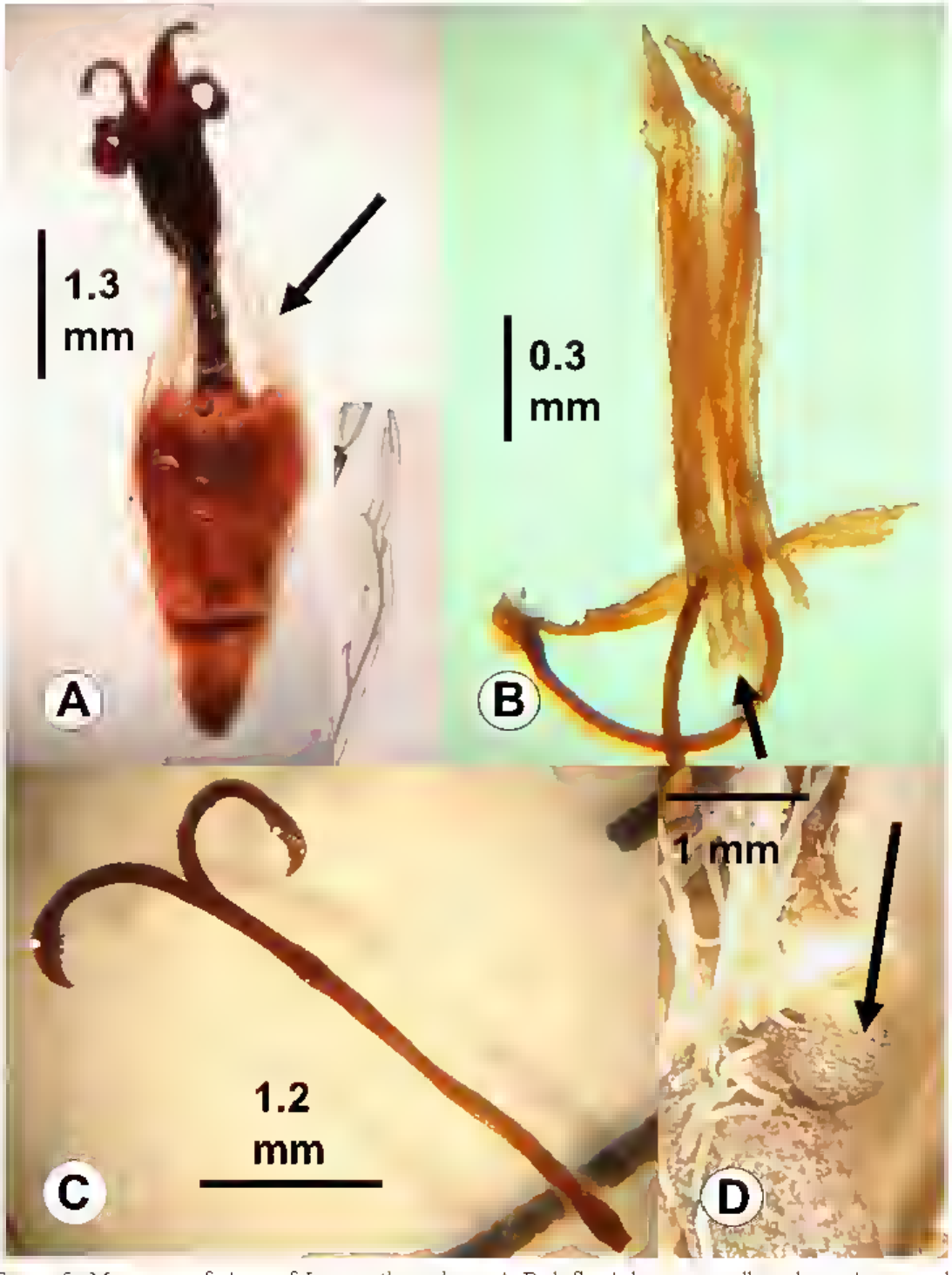

Figure 5 Microscopic features of *Lowryanthus rubens* A Disk floret showing corolla and immature cypsela The arrow points toward trichomes which in the close up are seen as biseriate with erect non diverging apical cells B Two post-anthesis stamens showing tailed anthers (arrow points toward the end of tails) C Bifid style D Close up of obcompressed nearly mature cypsela showing abaxial geniculate rostrum (arrow) (*Lowry et al 6648*, MO)

Malagasy *Lowryanthus* has paleate clinanthia, tailed anthers, style branches with 2-banded stigmatic surfaces, and obcompressed carbonized geniculate-rostrate cypselae (Figs. 2, 5D) and is a member of the Heliantheae Alliance (subfamily Asteroideae sensu Bremer 1994; Panero 2007a), but upon first dissection its tribal placement was not at all immediately apparent to me. Within Asteroideae, Inuleae (including Pluecheae) is the only traditionally recognized tribe characterized in part by consistently tailed anthers. It was basically similar to Inuleae, from which African-centered Athroismeae Panero, Cuban Feddeeae Pruski et al., and cosmopolitan Gnaphalieae Anderberg were segregated (viz Anderberg 1991; Cariaga et al. 2008; Panero 2005, 2007a, 2007b), and that is where the affinities of *Lowryanthus* were sought. *Lowryanthus* would be clearly anomalous, however, in either Feddeeae or Gnaphalieae.

Although the character of tailed anthers only places *Lowryanthus* somewhere in the general vicinity of Inuleae sensu lato (sensu Merxmüller et al. 1977) and segregate tribes, it is the very strange, obcompressed, carbonized, asymmetrically rostrate cypselae character (viz Eriksson, 1990, 1992, 1995; Figs. 2, 5D; described by Eriksson in 1990 as "abaxially curved") that specifically allows *Lowryanthus* to be placed near the genera of the African-centered *Blepharispermum* group, treated earlier by Merxmüller et al. (1977) as Inuleae.

The three genera of the *Blepharispermum* group (*Athroisma* DC., *Blepharispermum* Wight ex DC., *Leucoblepharis* Arn.) since have been placed in Heliantheae subtribe Ecliptinae (Eriksson 1990, 1991) as "unassigned to a subtribe" within tribe Heleniеae (Karis and Ryding 1994: 536) and based on molecular studies were placed in the newly described Athroismeae (viz Panero 2005, 2007a, 2007b). Panero (2005) expanded Athroismeae from 3 to 5 genera by adding the new monogeneric Centipedinae Panero and Anisopappinae Panero. Panero (2007b) added epaleate *Welwitschiella* O. Hoffm. to Anisopappinae, but Brouillet et al. (2009) placed this genus in Astereae. Ortiz (2010) described *Cardosoa* S. Ortiz, a sixth genus of Athroismeae. The present addition of *Lowryanthus* raises to 7 the number of genera (each monographed) recognized in the relatively small African-centered Athroismeae (Table 1), which contains 3 subtribes, 7 genera, and about 60 species. Subtribes, genera, species numbers, distributions, primary references, and a key to subtribes and genera of tribe Athroismeae follow.

Table 1. The subtribes, genera, species numbers, and distributions of Athroismeae.

I. Athroismeae	1. *Athroisma* DC. [as *Polycline* Oliv. in Humbert 1960–1963]	12 species, Africa, Madagascar, 1 sp. in Asia. (Eriksson 1995)
	2. *Blepharispermum* Wight ex DC.	15 species, Africa, Madagascar, Asia. (Eriksson 1992)
	3. *Leucoblepharis* Arn.	1 species, India. (Eriksson 1990).
	4. *Lowryanthus* Pruski	1 species, Madagascar. (Pruski 2014, present paper).
II. Anisopappinae	5. *Anisopappus* Hook. & Arn. [as *Epallage* DC. in Humbert 1960–1963]	17–40 species, Africa, Madagascar, 1 sp. in Asia. (Wild 1964, Eldenäs and Anderberg 1996, Ortiz et al. 1996, Ortiz 2005, Panero 2005).
	6. *Cardosoa* S. Ortiz.	1 species, Africa. (Ortiz 2010)
III. Centipedinae	7. *Centipeda* Lour.	10 species; mostly circumaustral, also Madagascar. (Walsh 2001, Nylinder et al. 2013).

Key to subtribes and genera of tribe Athroismeae (modified from Panero 2007b)

1. Cypselae brown to black, not carbonized, subterete to compressed.

2. Capitula disciform, epaleate; innermost disk florets 4-merous; cypselae epappose; (Centipedinae, 1 genus) ..... **Centipeda**
2. Capitula radiate, paleate; disk florets 5-merous; cypselae pappose; (Anisopappinae, 2 genera).

3. Capitulescence lax corymbiform; marginal florets radiate; disk corollas strictly actinomorphic; anther appendage acute apically; cypselae 10–20-costate ..... **Anisopappus**
3. Capitulescence racemiform-cymose; marginal florets subbilabiate; disk corollas slightly zygomorphic, anther appendage apiculate apically; cypselae < 10-costate ..... **Cardosoa**

1. Cypselae black, carbonized, obcompressed; (Athroisminae, three core genera + *Lowryanthus*).

4. Capitulescence open; capitula discoid; corollas red ..... **Lowryanthus**
4. Capitulescence of globose glomerules; capitula discoid or disciform; corollas mostly white.

5. Capitula 4–6-flowered; inner florets functionally staminate; cypselae pappose ..... **Blepharispermum**
5. Capitula 4–47-flowered; disk florets bisexual; cypselae epappose.

6. Capitula short-bracteate; twin trichomes of cypselae with diverging or recurved apices ..... **Athroisma**
6. Capitula long-bracteate; twin trichomes of cypselae with erect apices ..... **Leucoblepharis**

Within Athroisminae, the non-glomerate, red-flowered *Lowryanthus* is very different from the three other genera, each of which has densely glomerate, globose capitulescences and typically white corollas. However, by long marginal and apical twin trichomes on the epappose cypselae *Lowryanthus* is somewhat similar to *Athroisma* and *Leucoblepharis*. Additionally, *Leucoblepharis* has trinervate (vs. pinnately veined) leaves; *Blepharispermum* has occasionally thorny (vs. unarmed) stems, unisexual (vs. bisexual) disk florets, and cypselae with (vs. without) a true pappus of awns or scales; and *Athroisma* has diverging to recurved (vs. erect) apical cells of the twin trichomes of the cypselae, further distinguishing these three genera from *Lowryanthus*. The two non-typical subtribes have non-carbonized cypselae and either radiate capitula or innermost disk florets 4-merous, thereby differing from *Lowryanthus*.

I should also note here that the combination of morphological characters diagnostic for *Lowryanthus* is unmatched in any of the detailed regional treatments of Humbert (1923, 1960–1963), Hind et al. (1993), Beentje (2000, 2002), Beentje et al. (2005), and nothing similar can be found in the family overview of Bremer (1994). Thus, the striking *Lowryanthus rubens* is described as a new genus and species and placed in tribe Athroismeae. Molecular support of the affinities of *Lowryanthus* awaits study, which I suspect will show that a new subtribe is needed to accommodate *Lowryanthus*.

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I would like to thank Arne Anderberg (S) and Henk Beentje (K) for reviewing the manuscript; Henk van der Werff (MO) for correcting the Latin description; Porter P. (Pete) Lowry II (MO) for use of his field photographs; Pete Lowry, Guy Nesom, and Rosa Ortiz for helpful comments on the manuscript; Frédéric Tronchet (P) for sending me photographs of the specimens of *Lowryanthus* in P; and Cynthia Hong-Wa (MO) for helpful discussion and for sending me the base map used here.

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CAREX ×*CAYOUETTEI* (CYPERACEAE), A NEW INTERSECTIONAL SEDGE HYBRID FROM SOUTHERN QUÉBEC, CANADA

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ABSTRACT

A putative hybrid of *Carex* (Cyperaceae) was discovered in a swamp in the Montréal region (southern Québec, Canada). A survey of the surrounding vegetation, numerical phenetic analysis, and use of proxies of plant sterility showed that the individuals were sterile intersectional hybrids between sects. *Lupulinae* and *Vesicariae*. We propose the name **Carex ×cayouettei** A. Bergeron, **hybr. nov.** for the hybrid combination *C. comosa* × *C. lupulina*. Several factors (reproduction time, habitat and natural range) support the assumption that the hybrid is likely more common than suggested by previous knowledge, but difficulties encountered in identification may have limited documentation. This finding strengthens the evidence that *Lupulinae* and *Vesicariae* are closely related.

An unidentified sedge was discovered near a swamp during a survey of an urban forest in the metropolitan Montréal area. The plant did not resemble any known species of the region; we thus suspected that it was a natural hybrid. Initially, *Carex lupulina* and *C. pseudocyperus* seemed to be possible parents (authorities are given in Appendix 1), since both were found in the swamp near the unfamiliar sedge. Such a combination was nevertheless questionable because intersectional hybrids between sects. *Lupulinae* Tuck. ex J. Carey and *Vesicariae* (Heuff.) J. Carey [combined with sect. *Pseudocypereae* (Tuck.) Christ sensu Ball & Reznicek 2002] are uncommon (Cayouette & Catling 1992). In addition, visual analysis of the characters was problematic, particularly in relation to size of vegetative organs, which did not appear intermediate. Although hybrid vigor exists among sedges, the intermediate state or presence of some characters more related to one of the parents is essential to the determination of legitimate intersectional hybrids such as *C. lupulina* × *retrorsa* Schwein. (Dudley 1886; Cayouette & Catling 1992). We therefore examined the sedge vegetation around the unfamiliar plant more closely, and performed a phenetic analysis involving several other putative parents to determine which ones were involved in the hybrid combination.

Study site

The unidentified sedge was found at the Bois-de-Saraguay Nature-Park (45° 30.9' N, 73° 44.5' W), southern Québec, Canada. This Park is one of the best preserved urban forests on the Island of Montréal, not only because of restricted public access, but also because of its size (96 ha). This mature forest is characterized by a mosaic of mesic and hygric habitats with tree associations dominated by *Acer saccharum*, *Fagus grandifolia*, and *Tilia americana* on well-drained soils, swamps dominated by *Acer saccharinum*, and *Fraxinus pennsylvanica* on poorly-drained soils (Domon et al. 1986). In an exhaustive floristic survey (152 person-days) carried out by our research team between June and August 2011, a total of ca. 389 taxa were recorded, which represents a high level of richness for the region. Sedges accounted for a pool of 32 species (Appendix 1). Several rare Québec plants are only present in this park (Bergeron & Pellerin 2011; Bergeron et al. 2013). Despite low levels of past anthropogenic disturbances in this urban context, ca. 21% of florula is composed of naturalized and ephemeral plants.

Fieldwork and laboratory

During the plant survey of an open, flooded swamp on July 7, 2011, we collected the putative sedge hybrid for the first time. On July 14, 2011, we returned to the site to note all sedge species present in the swamp and within radii of 10 and 5 meters of the putative hybrid population. Macromorphological characters were measured *in situ* and *ex situ* on live specimens and those collected; the latter were then dried. Nine to twelve random measurements were taken for each character. In the laboratory, pollen grains were stained with cotton blue (lactophenol) to indicate defective cytoplasm. In order to collect the achenes, we examined the site closely a final time on October 16, 2011.

Phenetic analysis

After a summary examination of macromorphological measurements, we classified the putative hybrid as belonging to the group of "bladder" and "bottlebrush" sedges (sensu Hipp 2008). The specimens bore long and inflated perigynia, which distinguish the sect. *Lupulinae* and pistillate scales with scabrous awns characterizing, *inter alia*, the sect. *Vesicariae*. Furthermore, the broad vegetative blades on the putative hybrid could place it not far from the broadly construed sect. *Paludosae* (Heuff.) Christ (Ball & Reznicek 2002).

For phenetic analysis, we first checked the sedge list for the Bois-de-Saraguay (Appendix 1) to select the putative parents among *Carex* sects. *Lupulinae*, *Vesicariae*, and *Paludosae*. We included species belonging to the three sections, with the exception of *C. grayi* (globular spikes) and *C. pellita* (pubescent perigynia), which have characters too distant from the putative hybrid. Second, we included five species forming hybrid combinations according to Cayouette and Catling (1992) and with documented occurrences in the Montréal region and southern Québec (A. Bergeron, unpub. data; Brouillet et al., 2010+). *Carex lupuliformis* Sartwell ex Dewey was not selected due to its rarity and remote populations well-researched in the context of the Pellerin's team's project, "Rescuing false hop sedge" (Environment Canada 2014). Finally, we included three species exhibiting some ornamental qualities, unlisted for Québec but possibly present due to escape from cultivation. In order of selection as described above, the 13 species are the following: *C. intumescens*, *C. lacustris*, *C. lupulina*, *C. pseudocyperus*, *C. retrorsa*, *C. comosa* Boott, *C. hystericina* Muhl. ex Willd., *C. hirtida* Wahlenb., *C. utriculata* Boott, *C. vesicaria* L., *C. acutiformis* Ehrh., *C. gigantea* Rudge, and *C. hyalinolepis* Steud.

Measurements of macromorphological characters related to the 13 possible parents were compiled from the literature (Gleason & Cronquist 1991; Hill 2006; Ball & Reznicek 2002; Jones 2010). Data analysis was performed by Principal Coordinates Analysis (PCoA) with Caillez correction (Legendre & Legendre 2012, p. 493) on the mid-point of min and max values of each character. The PCoAs were calculated on character tables rescaled in Gower's dissimilarity matrix (Legendre & Legendre 2012, p. 278), and then multiplied with an *F*-ratio weighting (Adams 1972, 1982). With the min and max values of each character, an *F*-ratio (intergroup variance ÷ intragroup variance) was calculated from an ANOVA between the species. Derived from the literature, these ranges of values establish the true boundaries of the species, which guarantees the validity of the calculations even if the intragroup variance were computed on only two degrees of freedom. In fact, we also tried the PCoAs without weighting (Adams 1972, 1982), which did not alter our conclusions. However, the weighting with the *F*-ratios gave the greatest amount of explained variance on the first two PCoA axes, which justified the use of this procedure. Note also that these numerical methods are not statistical hypothesis tests. We used the weighted PCoAs to synthesize information and draw a conclusion based on decisions. All analyses were performed using the R language (R core team, 2013).

Preliminary analysis

Eighteen selected characters known to discriminate sedges within and between the three sections were used (Table 1) in a preliminary analysis which aimed to reduce the number of putative parents to be examined in detail. By excluding the putative hybrid, we calculated *F*-ratios for weighting each of the 18 characters (Table 1). Ordination of the first two PCoA axes with the 14 taxa including the putative hybrid (80% of explained variance) made it possible to segregate sedge sections and identify species with characters too distant from the putative hybrid. All members of sect. *Paludosae* were discarded. We then calculated two other PCoAs that led to the successive removal of species distantly related to the putative hybrid. The last preliminary PCoA was performed on seven taxa (94% of explained variance) and placed the putative hybrid approximately in the middle of the PCoA axis I, the *Lupulinae* being on one side and *Pseudocypereae* [incl. within sect. *Vesicariae*] on the other.

Triplet analysis

To show the intermediate state of the putative hybrid relative to the characters of two sedge species, we only retained the six most likely parents (*Carex comosa*, *C. gigantea*, *C. hystericina*, *C. intumescens*, *C. lupulina*, and *C. pseudocyperus*) found in preliminary analyses. For the final analyses, we included 23 characters to improve refinement of the differences between taxa, and calculated new *F*-ratios (by excluding the putative hybrid) for weighting each of these characters (Table 1). By considering one species of sect. *Lupulinae*, the putative hybrid, and one species of sect. *Pseudocypereae*, we performed nine weighted PCoAs i.e., on all possible combinations of triplets.

Table 1. Description of characters and units used in the phenetic analysis. The *F*-ratios calculated between the putative parents are also shown, i.e. with 13 species for preliminary analyses, and 6 species for triplet analyses

Characters	*F*-ratio for 13 spp.	*F*-ratio for 6 spp.
1. Culm length (cm)[*†]	0.0810	0.0433
2. Blade width (mm)[*†]	0.3396	0.2444
3. Number of prominent blade veins[*†]	0.5833	0.1200
4. Color of basal sheath (510 nm, 615 nm, 650 nm)[*†]	0.6360	1.1333
5. Number of terminal spikes[*†]	1.6005	0.9059
6. Sexuality of terminal spike (0: staminate, 1: bisexual)[*†‡]	0.9167	0.8000
7. Number of lateral spikes[*†]	0.1612	0.1294
8. Sexuality of lateral spike (0: pistillate, 1: bisexual)[*†‡]	0.7500	0.6000
9. Orientation of perigynium (45°, 90°, 135°)[*†]	6.8333	2.4000
10. Orientation of proximal spike (45°, 90°, 135°)[*†]	0.4028	0.2857
11. Perigynium length (mm)[*†]	2.4608	2.8642
12. Perigynium width (mm)[*†]	1.4872	2.3846
13. Perigynium length/width ratio	0.1435	0.1136
14. Length of perigynium beak (mm)[*†]	4.7309	5.2116
15. Length of perigynium teeth (mm)[*†a]	1.4347	1.6394
16. Number of perigynium veins[*†§]	0.9719	0.0342
17. Perigynium shape in cross section (0: trigonous, 1: round)[*†]	0.0581	0.1200
18. Apex of pistillate scale (0: acute, 1: acuminate, 2: awned)[*†]	0.6852	0.6000
19. Length of pistillate scale (mm)[*†]	NA	0.3613
20. Width of pistillate scale (mm)[*†]	NA	2.8887
21. Shape of beak teeth (0: straight, 1: outcurved, 2: very outcurved)[*†]	NA	4.2000
22. Width of proximal pistillate spike (mm)[*†‖]	NA	0.9464
23. Length of proximal bract (cm)[*†]	NA	0.4963

NA = Not applicable. [*]Characters measured directly on the putative hybrid. Data from [†]Ball and Reznicek (2002), [‡]Jones (2010), [§]Hill (2006), and [‖]Gleason and Cronquist (1991). [a]For *C. gigantea*, *C. lupulina* and *C. intumescens*, the length of perigynium teeth was measured in ImageJ (Rasband, 2012) on digital specimens after

imaging improvements (range between spp.: 0.5–1.2 mm); for each species, nine random specimens from AUA, TROY, USF, UWAL, or WIN herbaria (Thiers, 2008+) were used.

RESULTS AND DISCUSSION

The putative hybrid was discovered in a ca. 4000 m^2 swamp that was home to 10 species of sedges. The companion vegetation was mainly composed of hydrophytes e.g., *Alisma triviale*, *Impatiens capensis*, *Leersia oryzoides*, *Lemnoideae*, and *Onoclea sensibilis*. In an area of 314 m^2 (10 m radius) around the putative hybrid, we noted the presence of *C. cristatella* Britton, *C. intumescens*, *C. lupulina*, *C. pseudocyperus*, *C. tenera*, and *C. retrorsa*, while only three sedges were present in an area of 78.5 m^2 (5 m radius) i.e., *C. intumescens*, *C. lupulina* and *C. pseudocyperus*.

Two huge clumps of the putative hybrid, in full bloom, had established themselves in mud exposed to direct sunlight (Fig. 1); they were spread over an area of 90 cm by 80 cm and 110 cm by 70 cm, respectively. Clumps of other sedges found in the swamp were smaller, suggesting that the putative hybrid might imply a larger and not inventoried species. No achene was found on the *in situ* specimens or those collected. In the laboratory, the test of pollen colorability with cotton blue was 0%. Grains and their walls were deformed. Anthers were not exserted in the staminate spikes, or the staminate portions of the androgynous spikes. When we returned to the site in October, all infructescences of the two clumps were aborted, whereas achenes were well-developed on the surrounding sedges.

Figure 1. One of the huge clumps of the putative sedge hybrid found in full bloom in an open swamp at the Bois-de-Saraguay Nature-Park (southern Québec), on July 14, 2011.

Examination of 9 triplets using ordinations showed that the first PCoA axes explained the greatest amount of variance (55.8% to 84.2%), which usually located the putative hybrid in the middle of the diagrams. The second axes mostly showed the distinct nature of the putative hybrid by positioning it at one end, and the various putative parents at the other end. Comparison of 9 triplets (Fig. 2) revealed that the "com–hyb–lup" combination explained the most variance, and this combination placed the two species practically equidistant from the putative hybrid on PCoA axis I.

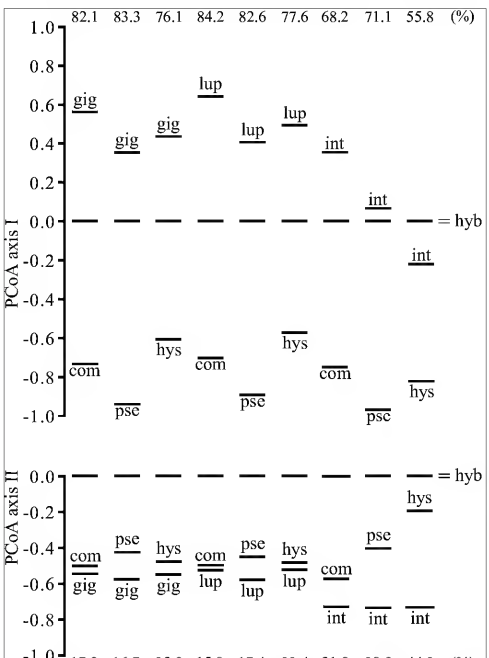

Figure 2. Results of the nine PCoAs performed on the species-by-character tables, rescaled into Gower's dissimilarity matrices and weighted by the *F*-ratios. The upper part of diagram shows the scores (horizontal bar) obtained for each of the nine PCoA axis I, while the lower part shows the scores for each of the PCoA axis II. The putative hybrid (hyb) was located at zero coordinates. The explained variance (%) per axis and for each triplet analysis is shown. The species codes correspond to the first three letters of their specific epithets.

The proxies of sterility (i.e., uncolored grains, undeployed anthers, aborted infructescences) and the set of intermediate characters in the PCoAs confirmed that the taxon was an intersectional hybrid between one smaller *Lupulinae* parent, and one large *Vesicariae* parent. The triplet analyses revealed that the correct hybrid combination (most equidistant position) was *Carex comosa* × *lupulina*. *Carex pseudocyperus* is not involved in the combination, although it was observed a few meters from the hybrid. In fact, visual examination of specimens from the Montréal region (Marie-Victorin Herbarium, MT) showed us that the blade widths of the hybrid (ca. 6–17 mm) were consistent with the morphometry of *C. comosa* (sometimes >13 mm) but not with that of *C. pseudocyperus* (always ≤13 mm). Qualitatively, the broad base of the culm of the hybrid is very similar to that of *C. comosa* in regard to width, texture, and color. Fernald (1950) as well as Cayouette and Catling (1992) have mentioned the combination *C. comosa* × *lupulina*, but there is currently no binomial name. Difficulties encountered in identification may have limited documentation, but it is possible that this taxon is more widespread than suggested by previous knowledge. To help in identification, we provide the morphological description below. Some additional measurements were taken on type specimens.

Carex ×cayouettei A. Bergeron, **hybr. nov**. Figures 1, 3, 4. **TYPE: CANADA. Québec**. Ville de Montréal: Bois-de-Saraguay dans un marais eutrophe, 508424 mE, 5041055 mN (UTM 18T, NAD 83), 14 Jul 2011, *A. Bergeron, M. Charrier, J.-S. Mignot,* & *E. Bergeron 11104* (holotype: MT; isotype: MICH); 7 Jul 2011, *SP069* (paratype: DAO).

Plants cespitose. **Culms** 69–95 cm, scabrous distally. **Leaves**: basal sheaths brownish; blades mid to dark green, flat to W-shaped, 6–17(–19) mm wide. **Inflorescences**: peduncles of proximal spikes 0.9–3.5 cm, scabrous distally; proximal bract 37–53 cm, much longer than inflorescence, blades 6–11 mm wide, glabrous. **Spikes**: lateral 1–3 spikes androgynous, or pistillate, ascending to arching, 85–150-flowered, cylindrical, 45–80 × 16–19 mm; terminal 1–2(–3) spikes staminate, the proximal (if present) often ± forked and androgynous (but few perigynia at the base), 35–64 × 2.5–3.5 mm. **Staminate scales** scabrous-margined. **Pistillate scales** narrowly lanceolate, 6–8.5 × 0.8–1.5 mm, green center with subciliate hyaline margins, sometimes brown colored, apex scabrous-awned. **Perigynia** ascending to spreading, strongly 14–19-veined, slightly stipitate, lance-ovoid, inflated, trigonous to subcircular in cross section, 8–11 × 2.5–3.5 mm; beak, 4–6 mm, bidentate; teeth, fairly straight, 0.5–1.3 mm. **Stigmas** 3. **Achenes** aborted.

The taxon is named in honor of the Québec botanist Jacques Cayouette, who has devoted his life to studying graminoid plants and, in particular, sedge hybrids.

Distinguishing characteristics

Among its congeners, *Carex* ×*cayouettei* is placed in sedges with culms and blades reaching a large size; with several spikes per culm having flowers either unisexuals or bisexuals, and bearing perigynia with a glabrous body and 3 stigmas. The pale brown basal sheaths and awned pistillate scales make this nothospecies similar to *C. comosa* from which it differs by its straight and shorter teeth of the perigynium; these latter characters are instead similar to *C. lupulina*. Macromorphological characters with an intermediate state relative to both parents are mainly related to the width and length of the perigynia and their beaks as well as the orientation of the perigynia along the axes of the pistillate spikes (Table 2). Some lateral (or even terminal) spikes of *C.* ×*cayouettei* are androgynous, which is sometimes observed in *C. comosa* (Hipp 2008). Similarly, the sedge hybrid most frequently bears 2(–3) terminal spikes, which is also sometimes observed in *C. lupulina* (but rarely according to Mohlenbrock 2011). Thus, an interesting feature of *C.* ×*cayouettei* is that it expresses sexual traits only occasionally encountered in both parents.

Table 2. The most distinguishing characteristics of *Carex ×cayouettei* relative to its parents (*C. comosa* and *C. lupulina*). See Table 1 for data sources.

Characters	***C. comosa***	***C. ×cayouettei***	***C. lupulina***
Color of basal sheath	Brownish	Brownish	Reddish to brownish
Apex of pistillate scale	Awned	Awned	Acute to awned
Shape of beak teeth	Very outcurved	Straight	Straight
Length of perigynium teeth	1.3–2.8 mm	0.5–1.3 mm	0.5–1.1 mm
Length of perigynium beak	2–3.8 mm	4–6 mm	6–10 mm
Perigynium length	4.8–8 mm	8–11 mm	11–19 mm
Perigynium width	1.1–1.8 mm	2.5–3.5 mm	3–6 mm
Orientation of perigynium	Spreading to reflexed	Ascending to spreading	Ascending

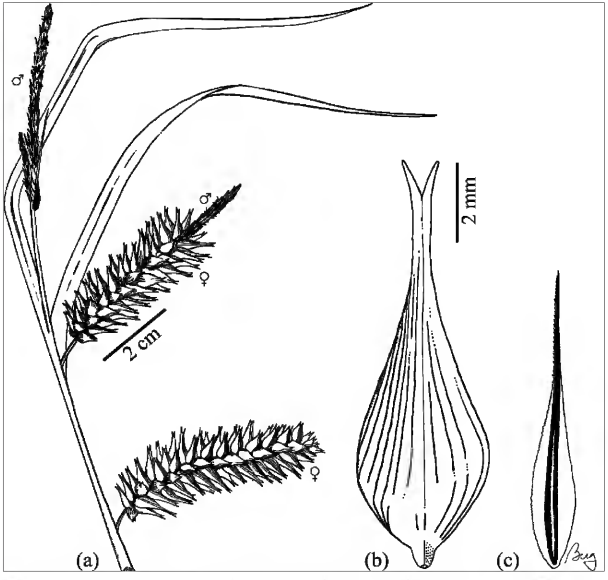

Figure 3. Illustration of *Carex ×cayouettei* showing (a) the inflorescence with terminal staminate spikes and lateral androgynous and pistillate spikes (b) the perigynium, and (c) the pistillate scale

Figure 4 Holotype of *Carex* ×*cayouettei* A. Bergeron

Carex ×*cayouettei* is likely a true sterile hybrid with parents, *C. comosa* (n = 32) and *C. lupulina* (n = 28−30), having sets of chromosomes of a slightly different count (Wahl 1940; Reznicek & Ball 1974). This suggests that the genome of *C.* ×*cayouettei* contains irregular meiotic chromosome associations contributing to its complete sterility, as is observed in hybrids of different sections (Cayouette & Catling 1992; Hipp et al. 2009) although some taxa of this kind (e.g., *C.* ×*langeana* Fernald) can produce achenes in rare circumstances (J. Cayouette, pers. comm.). Further research is needed to verify this point. The sterility of intersectional hybrid sedges acts as a barrier to dispersal of these taxa, which explains their sporadic distribution. Thus, the presence of *C.* ×*cayouettei* individuals in a given place requires a hybridization event. The likelihood of the occurrence of such events may be more common than suggested by previous knowledge. First, there is a time window, from late-spring until mid-summer, where the reproduction periods of both parents match (Ball & Reznicek 2002). Second, both parents share the same habitat types (e.g., swamps, wet meadows); and third, their respective natural ranges are similar and of considerable size. Indeed, *C. comosa* and *C. lupulina* are obligate wetland species (Lichvar 2013) distributed together at least throughout eastern North America, i.e., from Texas to southern Québec (Ball & Reznicek 2002; NatureServe 2013).

Hence, the discovery of mature individuals of *Carex* ×*cayouettei* in a Bois-de-Saraguay swamp indicates that a hybridization event between both parents occurred precisely at this location. Several reasons could explain the absence of *C. comosa* from our floristic inventory. It is possible that the population of this species sensitive to fluctuations in hydrology (NatureServe 2013) has become locally extinct, because the swamp has been profoundly altered by beavers in recent years (A. Bergeron, unpub. data). However, the most plausible explanation is that *C. comosa* remained unnoticed during our fieldwork. It is not unusual for individuals of *C. comosa* bearing narrow pistillate spikes to be interpreted as *C. pseudocyperus* (Bicknell 1908), especially since these two species often grow together (Ball & Reznicek 2002). Moreover, it appears that the invasion strategy of *C. comosa*, a species that can live at least 20 years, is to remain in a vegetative state for a few years before reproducing (Bernard & Seischab 1994). Without a fruiting structure, it can be difficult to properly document the occurrence of *C. comosa*. Its presence in the Montréal region has nevertheless been confirmed by herbarium data (Brouillet et al. 2010+), and it was recently observed in a marsh located ca.10 km from Bois-de-Saraguay (A. Bergeron, pers. obs.).

There is little doubt that scant documentation of *Carex* ×*cayouettei* is largely related to difficulties in identifying it formally. Also, it may be that some botanists aware of the parasitic deformities sometimes found on perigynia of the *Lupulinae* species have assumed that it was such an individual (Reznicek & Ball 1974). To complicate matters, the absence of flowering individuals of *C. comosa* in the vicinity of the hybrid can also lead botanists to false interpretations, as was our case, and moreover, it is possible that the hybrid remains vegetative for many years, like its parent. This feature could contribute to maintaining populations of the hybrid and also could make it a good candidate for inclusion among horticultural plants used in plant engineering or in landscaping of artificial ponds.

Finally, studies of intersectional hybrids have often contributed to revealing the taxonomic relationships within the genus *Carex*. In particular, it is known that *C. lupulina* hybridizes with *C. hurida*, *C. retrorsa*, or *C. vesicaria*, which indicates the affinity between the sects. *Lupulinae* and *Vesicariae* and their positions in a larger group (Reznicek & Ball 1974; Menapace & Wujek 1987; Ball & Reznicek 2002). The documentation of *C.* ×*cayouettei* is further evidence of the phylogenetic relatedness between these two sections.

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Appendix 1. Sedges found in the Bois-de-Saraguay Nature-Park.

Carex albursina E. Sheld.
Carex alopecoidea Tuck.
Carex bebbii (L.H. Bailey) Olney ex Fernald
Carex blanda Dewey
Carex bromoides Schkuhr ex Willd.
Carex cephaloidea (Dewey) Dewey
Carex crinita Lam.
Carex cristatella Britton
Carex deweyana Schwein.
Carex echinodes (Fernald) P.E. Rothr., Reznicek & Hipp
Carex gracillima Schwein.
Carex granularis Muhl. ex Willd.
Carex grayi J. Carey
Carex grisea Wahlenb.
Carex hirtifolia Mack.
Carex intumescens Rudge
Carex lacustris Willd.
Carex leptonervia (Fernald) Fernald
Carex lupulina Muhl. ex Willd.
Carex pedunculata Muhl. ex Willd.
Carex pellita Willd.
Carex plantaginea Lam.
Carex projecta Mack.
Carex pseudocyperus L.
Carex radiata (Wahlenb.) Small
Carex retrorsa Schwein.
Carex rosea Schkuhr ex Willd.
Carex stipata Muhl. ex Willd.
Carex tenera Dewey
Carex tribuloides Wahlenb.
Carex typhina Michx.
Carex vulpinoidea Michx.

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LARGE INEQUALITIES IN HERBARIUM SPECIMEN DENSITY IN THE WESTERN UNITED STATES

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ABSTRACT

Herbarium specimen records from 11 western states of the USA are assayed (5.6 million specimen records obtained from on-line databases). On a county basis, specimen density varies considerably, by a factor of ~2500 (highest in San Francisco County, California, at 99.2 specimens/km^2; lowest in Blaine, Liberty, and Prairie counties, Montana, at 0.04 specimens/km^2). California exhibits the highest specimen density, nearly 2x higher than the second highest state (Wyoming). All states except Nevada have one to several counties which fall above the 80th percentile for density. Many states have large areas below the 20th percentile. Specimen density is correlated with human population density. Large areas deficient in specimen records indicate challenges for vascular plant systematics and conservation. A comprehensive, adequately funded program of floristic exploration in the western USA would require gathering of an additional ~1.5-2 million specimens to minimally rectify the observed inequalities.

Herbarium specimens are the fundamental currency of biodiversity studies. In the intellectual economy of biological systematics, classifications are products, specimens their raw materials. In the USA, herbaria have made great progress in digitization of specimen records in their holdings, supported by modest funding. Production of regional floras such as the revised *Jepson Manual* (Baldwin et al. 2012) and Flora North America North of Mexico (FNA 1993-2006) have been greatly facilitated by digitization of herbarium records. However, the increased access to digitized specimen records is in contrast to the overall decline in specimen collecting (Prather et al. 2004a,b; Tewksbury et al. 2014).

This paper identifies a significant inequality of herbarium specimen density in the western USA, based on accession of digitized records.

Methods

I queried on-line specimen databases for herbarium records of vascular plants by county for the 414 counties in 11 western USA states between 10 January and April 4, 2014. Records from regional consortia were tallied first (Consortium of California Herbaria, Consortium of Pacific Northwest Herbaria, Southwest Environmental Information Network), then records from larger individual herbaria were added (CAS, RM, COLO, MINN and MO-Tropicos — herbarium abbreviations follow Thiers 2014). Queries were structured to eliminate specimen records offered by more than one data provider across platforms. Data on spelling of county names, state and county land surface areas, and human population density (2010 census) were obtained from Wikipedia (accessed January 2014). Several variant county spellings were corrected in the queries. Minor internal inconsistencies in the area of counties and states were not corrected (these in no case are greater than about 20 km^2). Presentation and analysis of the data is given as percentiles for simplicity of comparisons.

Results and discussion

Observed specimen density (specimens/km^2) differs by a factor of 2480, ranging between 99.2 (San Francisco County, California) to 0.04 (Blaine, Liberty, and Prairie counties, Montana). Using the breakdown criteria of Tukey (1977), 33 counties are outliers relative to the other 381 counties: all outliers are enriched in specimen density. The mean specimen density of these 33 enriched outliers is 12.27 specimens/km^2. The mean for the 381 counties that are not outliers is 1.65 specimens/km^2, smaller by a factor of 7. Figure 1 provides a frequency distribution of the density for the 414 counties: the distribution is highly left-skewed.

The inequalities in specimen density have a strong geographic pattern (Figure 2, Table 1). Relative to other states, California is well-collected, with an average density of 4.76 specimens/km^2 (1.9 million digitized specimen records). Allowing for the fact that California herbaria are not yet fully digitized (CAS and DAV remain to finish), the actual density might approach 6 specimens/km^2 (based on reported *Consortium of California Herbaria* digitization progress reports). By contrast, Montana and the Great Basin states of Nevada and Utah are comparably depauperate (Table 1).

All states have both well-collected (defined as >80th percentile) and under-collected <defined as <50th percentile) counties (Figure 2). Some of the deficient counties are remote from population centers (Utah, Carbon, and Emery counties; Nevada, all but Carson City; Crook County, Oregon, etc., cf. Figure 2). Other deficient regions include counties with a large fraction of the land area devoted to agriculture (e.g. Jerome and Minidoka counties, Idaho; counties in eastern Colorado). Other deficient counties, although agricultural, include sizeable remnants of non-managed vegetation (most of the deficient counties in Montana; Jefferson County in Idaho; Adams, Franklin, and Lincoln counties in Washington). The frequent low specimen density in rural counties also suggest that weed records might be disproportionately lacking therein.

Regression analysis identified a significant correlation between specimen density and density of human population based on the 2010 census (R^2 0.66, $p<0.001$) — counties with a greater human population are well-collected compared to sparsely populated counties. Moreover, the geographic location of enriched vs. deficient counties suggests that proximity to herbaria and universities, which are located in population centers, is important. Such a pattern is not that unexpected: botanists gather specimens close to home.

The western USA states fall perhaps into three groups (Table 1). California, Colorado, and Wyoming have high to moderate specimen density, Washington and Arizona intermediate density, with the remaining states trailing behind (Nevada far in the rear).

Table 1 summarizes two potential criteria upon which the adequacy of regional specimen density could be assessed. If states are judged relative to a performance standard based on the mean specimen density for California, nearly 9 million additional specimen records would be necessary to attain this data density elsewhere over the region. Alternatively, if states are judged against the 70th percentile for non-California counties (about 2 specimens/km^2), the resultant specimen deficit is a mere 1.8 million specimens (Table 1). By this latter standard California, Wyoming, and Colorado are well-collected, with Washington, Arizona, Idaho, Oregon, New Mexico, Utah, Montana, and Nevada deficient to varying degrees.

For convenience, readers who know the specimen number or density for a particular county can approximate percentile using the regression equation: percentile = 0.2246ln (density) + 0.4251 (r^2=.939)

	Specimen Density (sheets/km2)					Deficit Comparison	
STATE	Mean	High	Low	Specimens	Area (km^2)	Calif. Standard	70% tile Non-CA Standard
California	**4.76**	99.19	0.35	1,922,851	404,224	0	+1,118,445
Wyoming	**2.75**	5.82	0.83	695,570	253,348	-510,366	+191,407
Colorado	**2.30**	14.74	0.06	620,782	269,837	-663,642	+83,806
Washington	**1.92**	26.84	0.03	355,227	184,827	-524,550	-12,579
Arizona	**1.84**	6.21	0.67	542,300	295,234	-863,014	-45,216
Idaho	**1.43**	7.58	0.08	310,419	216,632	-720,749	-120,679
Oregon	**1.34**	10.73	0.36	340,518	255,026	-873,406	-166,984
New Mexico	**1.01**	10.98	0.05	317,580	315,194	-1,182,743	-309,656
Utah	**0.82**	3.76	0.16	179,546	219,887	-867,116	-258,029
Montana	**0.81**	4.86	0.04	310,181	380,800	-1,502,427	-447,611
Nevada	**0.34**	2.25	0.13	96,696	286,367	-1,266,411	-473,174
Grand Mean	**1.77**			**5,691,670**	**3,081,376**	**-8,974,425**	**-1,833,927**

Table 1. Number of databased specimens by state, specimen density, and deficit comparisons based on the specimen density for California, and for the 70th-percentile county density for non-California counties.

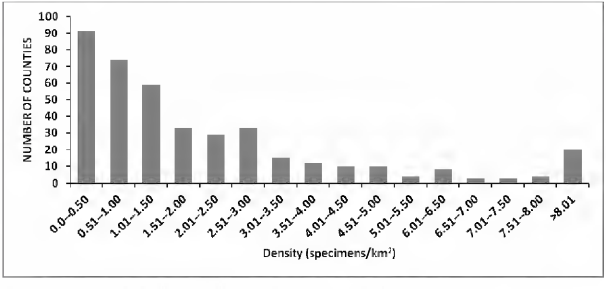

Figure 1. Frequency distribution of specimen density for 414 counties in 11 western states of the USA. The distribution is strongly left-skewed (the mean density is 1.77, Table 1).

Arizona – Only one county, the smallest in the state, Santa Cruz County, is well-collected, with adjacent Pima and Cochise counties intermediate. Notable in this region are the high mountains with Madrean floristic affinities (McLaughlin 1994), which are regarded as a biodiversity hot-spot (Mittermeier et al. 2011) and which are under active study (see Felger et al. 2014). Two of the deficient counties (Yuma and La Paz) are in the western Sonoran desert region: adjacent Imperial County, California, and Clark County, Nevada, have similarly low density, making a regional deficiency. Navajo County is likewise deficient — its far northern portion is included in the recent *Four Corners Flora* (Heil et al. 2013).

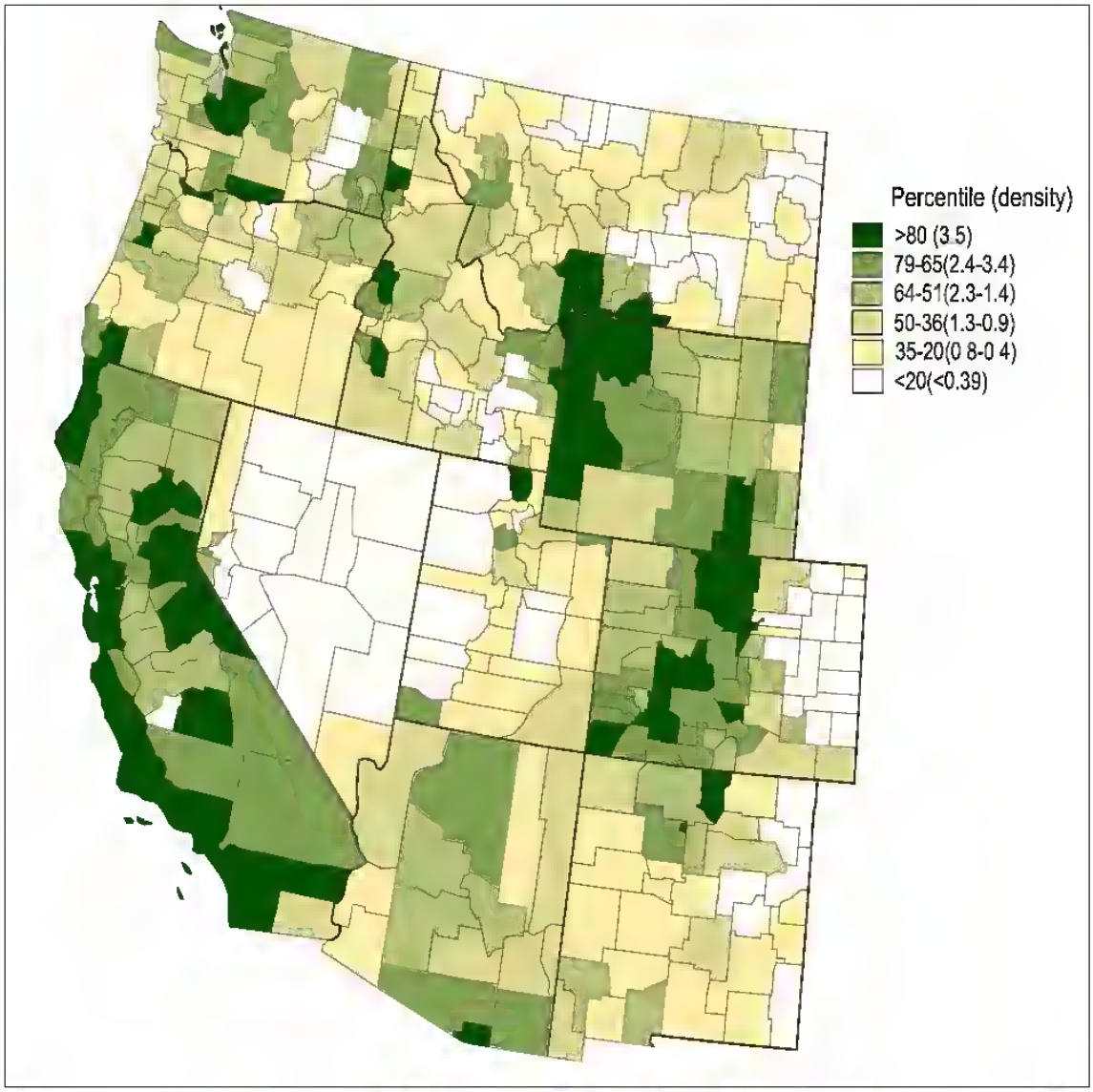

Figure 2. County map of the western United States showing herbarium specimen density (6 mapped categories based on percentile of observed county density variation).

California - In California, which is generally well-collected, Kings County stands out as one of the least collected counties in the western USA (0.32 specimens/km^2, 15th percentile). It would be attractive to attribute the lack of specimens from Kings County to the fact that a large portion of the county lies in the San Joaquin Valley, the most intensively agrarian landscape in North America (Preston 1981). However, the western third of the county is mountainous, situated in the inner South Coast Ranges, suggesting the lack of specimens is not due to a lack of species richness in the flora. The recently described monotypic Brassicaceae genus *Twisselmannia* (Al-Shebaz 1999), a narrow endemic to Kings County, suggests that the low collection density for that county may owe, at least in part, to under-collection.

The map in Figure 2 shows that California contains a disproportionate number of well-collected counties. Moreover, non-political geographic subdivisions of the state are also high density outliers: Yosemite National Park (33,214 specimens) has a density of 11 specimens/km^2, equal to 97th percentile for counties. Yosemite Valley (±20 km^2, 5843 specimens) has an extreme density, about 275 specimens/km^2. The California Channel Islands are also all extreme high density outliers: Anacapa Island (911 specimens/km^2), Santa Barbara Island (488), Santa Cruz Island (87), Santa Catalina Island (60), San Nicolas Island, and Santa Rosa Island (28 specimens/km^2) all exceed the 99th percentile equivalent for county density.

Colorado – third to California in collection density (Table 1), the strong pattern of well-collected counties in the mountains along the Front Range and in the headwaters Colorado River basin is in direct contrast to the poorly collected counties in the eastern Great Plains. Eleven counties exceed the 90th percentile: Gilpin, Boulder, Clear Creek, San Juan, Grand, Denver, Lake, Larimer, Gunnison, Jackson, and Jefferson. Although the recently published *Four Corners Flora* (Heil et al. 2013) covers a geographic region where some of the counties are well-collected, overall the collection density of that flora region averages the 58th percentile. The eastern plains portion of the state average in the 7th percentile (in this region, Otero County is better collected, 51st percentile). These eastern counties are largely agricultural and sparsely populated: low specimen density is opposed to the prevalence of grazing lands used for intensive livestock grazing, suggesting poor floristic documentation. The same west to east gradient in specimen density is also seen in adjacent New Mexico.

Idaho – overall collecting density is more uniform than adjacent states, but most counties fall in the lower range (<50th percentile). Overall, the density pattern is similar to Oregon, but there are still several marked inequalities. The low collection density in the western portion of the Snake River plains (Lincoln, Jefferson, Minidoka, and Jerome counties) indicates a significant regional deficit, perhaps attributable to an intensive agricultural district. The high concentration in Latah County (85th percentile) is part of a regional pattern connected to adjacent Washington (associated with proximity to WTU and nearby ID/IDF).

New Mexico – almost all of the state falls below the 35th percentile, with the far eastern portion below the 20th percentile (the easternmost deficient counties mirror the same pattern in Colorado). The sole well or moderately collected counties are in the north in the Rocky Mountains.

Nevada – relatively a 'third-world' state, the least collected state of any in the western USA. The recently finished *Intermountain Flora* (Holmgren et al. 2012) essentially covers most all the white space of the map in Figure 2. It should be noted that digitized specimen records for the *Intermountain Flora* region concentrate on the last two published volumes (Holmgren et al. 2005, 2012) and as such, on-line specimen density for the region is artificially low, although it is unlikely to be of notable greater overall magnitude. The only counties with even a modicum of specimen density are those in the Sierra Nevada and its eastern foothills adjacent to California (Carson City, Douglas. and Storey counties, in the Reno region).

Montana – herbarium specimen density for most of the state is dismally low, relatively. Half of the counties in the state are below the 20th percentile, and nearly 90% of the state is below the 50th percentile. Only three counties (Carbon, Gallatin, and Park) have high density (>80th percentile), these in the Rocky Mountains (proximal to MONT and more significantly RM) and adjacent to much better collected Wyoming. The large deficient counties are sparsely populated but are not entirely given over to intensive agriculture; they retain sizable remnant habitat areas of non-managed vegetation.

Oregon – specimen density is most distinctly divided regionally west and east of the Cascades, with the highest density in urban Multnomah and Benton counties (vicinity of ORE/OSU). The far southwestern counties (Josephine, Curry, and Jackson) are well-collected, being part of the California Floristic Province. The moderate density in the Wallowa Mountains of the far northeast is also of note.

Utah – significantly under-collected relative to the overall mean density (Table 1). The only two counties with high density (Daggett and Cache) are in the Wasatch Mountain province. Washington County in the far southwest is moderately well-collected, at 74th percentile. Most of the Bonneville Basin in the western half of the state is very significantly under-collected (<20th percentile). The state flora, now in its 4th revision (Welsh et al. 2008), indicates slow but steady progress in floristic documentation, but the low overall collection density suggests opportunities for fruitful future floristic exploration.

Wyoming – the second best collected state in the data set. The 6 counties that comprise the Rocky Mountain portion of the state – Teton, Albany, Park, Sublette, Lincoln, and Crook, form a large well-collected block exceeding the 80th percentile. By comparison to other western states, Wyoming has comparably few poorly collected counties: Niobrara County is the lowest at the 33rd percentile. Compared to ecologically similar Montana, the differences in collection density amongst comparable physiographic regions in the two states are manifold.

Conclusions

Large areas of the North American continent extremely deficient in herbarium specimen records indicate significant challenges for vascular plant systematics and conservation in the USA. Bebber et. al (2010, 2012) have quantitatively demonstrated that description of new species of vascular plants is disconnected from their initial discovery. That is, new species are most often "discovered" in herbaria — specimens of undescribed taxa reside in collections for several decades before they are recognized and treated and their initial recognition requires a threshold number of accumulated specimens. The nearly 2500-fold difference in collection density reported in this paper strongly implies that undiscovered plant diversity in under-collected regions is concealed. Given this, going forward, preparation of floristic treatments will suffer from the unequal distribution of specimens.

Bebber et al. (2012) also have shown that contribution of type specimens is non-randomly distributed among collectors. Their analysis of the dynamics of plant collecting shows that long apprentice times are required to develop expertise in floristic botany. Accordingly, the apparent decline in practicing taxonomists (Whitfield 2012; Bacher 2012) is in stark contrast to the large large, under-collected areas of Figure 2. Who will collect the requisite 2 million specimens to fill in the map?

The fact that California is disproportionately collected relative to the 10 other western USA states — arguably 'over-collected' — would seem to indicate that no further specimens need be gathered there. That such a view would be folly has been convincingly demonstrated by Joppa et al. (2011), who show that biodiversity 'hot-spots' house most undescribed plant species. The California region is such a 'hot-spot' of vascular plant diversity. In the roughly two decade interval between the 1st and 2nd editions of the *Jepson Manual* (Hickman 1993; Baldwin et al. 2012), about 163 new California endemics were described, and about 373,000 additional accessions were made after initial publication of a revised, modern flora (specimen data estimate based on *Consorttum of California Herbaria*). Even well-collected California needs attention from floristic botanists.

Common sense indicates that it is unlikely that botanists can muster the effort, given available resources, to gather 9 million additional specimens from the western USA. I believe, however, that it

is not unrealistic to gather and/or database an additional 1.8 million regional specimens (to equal the 70th-percentile standard, see Table 1). Attaining such a goal would require significant increase in floristic field studies, with increased and adequate funding. A comprehensive, adequately funded program of floristic exploration in the western USA is necessary to rectify the observed inequalities.

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A NEW OCELLATE SPECIES OF *MATELEA* (APOCYNACEAE, ASCLEPIADOIDEAE) FROM MESOAMERICA

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ABSTRACT

Matelea corniculata W.D. Stevens & Arbeláez, **sp. nov.** (Apocynaceae, Asclepiadoideae, Gonolobinae), from the Caribbean forest of Costa Rica and Nicaragua is described. It is a member of a loose assemblage of small-flowered species held together primarily by having a bright white, reflective ocellus at the tip of each corolla lobe. A description, diagnosis, and illustration are provided.

Matelea Aubl., as circumscribed by Woodson (1941), probably comprises 200 to 300 species of the American tropics and subtropics and has been the catch-all genus of the group now known as the Gonolobinae. Efforts to tease phylogenetically meaningful genera from Woodson's "Matelea" have proceeded slowly, but several segregate genera have achieved some currency. *Matelea* in the strictest sense comprises a dozen or two species in the Amazon basin (Farinaccio & Stevens 2009).

The "ocellate complex" (Krings 2012) of *Matelea* is a loose assemblage of small-flowered species held together primarily by having a bright white, reflective ocellus at the tip of each corolla lobe. There are five species of this complex in the Caribbean (Krings 2011), one in Venezuela (Krings 2012), and with this new species five in Mesoamerica. Although there is a great deal of variation in the floral morphology within these eleven species, the three species with known fruits, all Caribbean, have peculiar, narrow, 5-ridged follicles that match nicely the follicles of the type elements of *Matelea*. The phylogeny of the Gonolobinae is far from being resolved and seems to become less rather than more clear as molecular data accumulates, but it is easy to imagine that a circumscription of *Matelea* only slightly expanded from the type elements could include this "ocellate complex."

Matelea corniculata W.D. Stevens & Arbeláez, **sp. nov.** **Type: COSTA RICA. Heredia.** Finca La Selva, Puerto Viejo de Sarapiquí, Sábalo-Esquina Trail, 2000 Line, first growth, creek bank, 7 Jul 1979, *J. Sperry 840* (holotype: DUKE; isotype: MO). Figure 1 A-D.

This new species is most similar to *Matelea emmartinezii* W.D. Stevens but differs conspicuously in having a strongly convex (not more or less plane) style apex, a well differentiated, 5-lobed outer corona (rather than a simple pentagonal disk), and corolla lobes that are longer, plane and with prominent horns between the corona lobes (rather than shorter, cucullate and lacking horns).

Woody twining vine with thick, tan-colored, fissured cork, latex unknown. **Stems** with a mixed indumentum in 2 rows, long trichomes reflexed, 0.3–0.6 mm, pale brown, tips straight, capitate-glandular trichomes ca. 0.05 mm, brown, internodes 2–10 cm. **Leaves** opposite, blades ovate to elliptic, 4.5–11.0 x 1.5–6.5 cm, apex acuminate to long-acuminate, base rounded or shallowly cordate, adaxially smooth, glabrous or with a few glandular trichomes at the base of the midrib, abaxially pusticulate, glabrous except with sparse glandular trichomes on veins, lateral veins 4 to 5 pairs, curved, middle veins 30°–45° to midrib, colleters 2; petioles 0.4–1.2 cm, with dense glandular

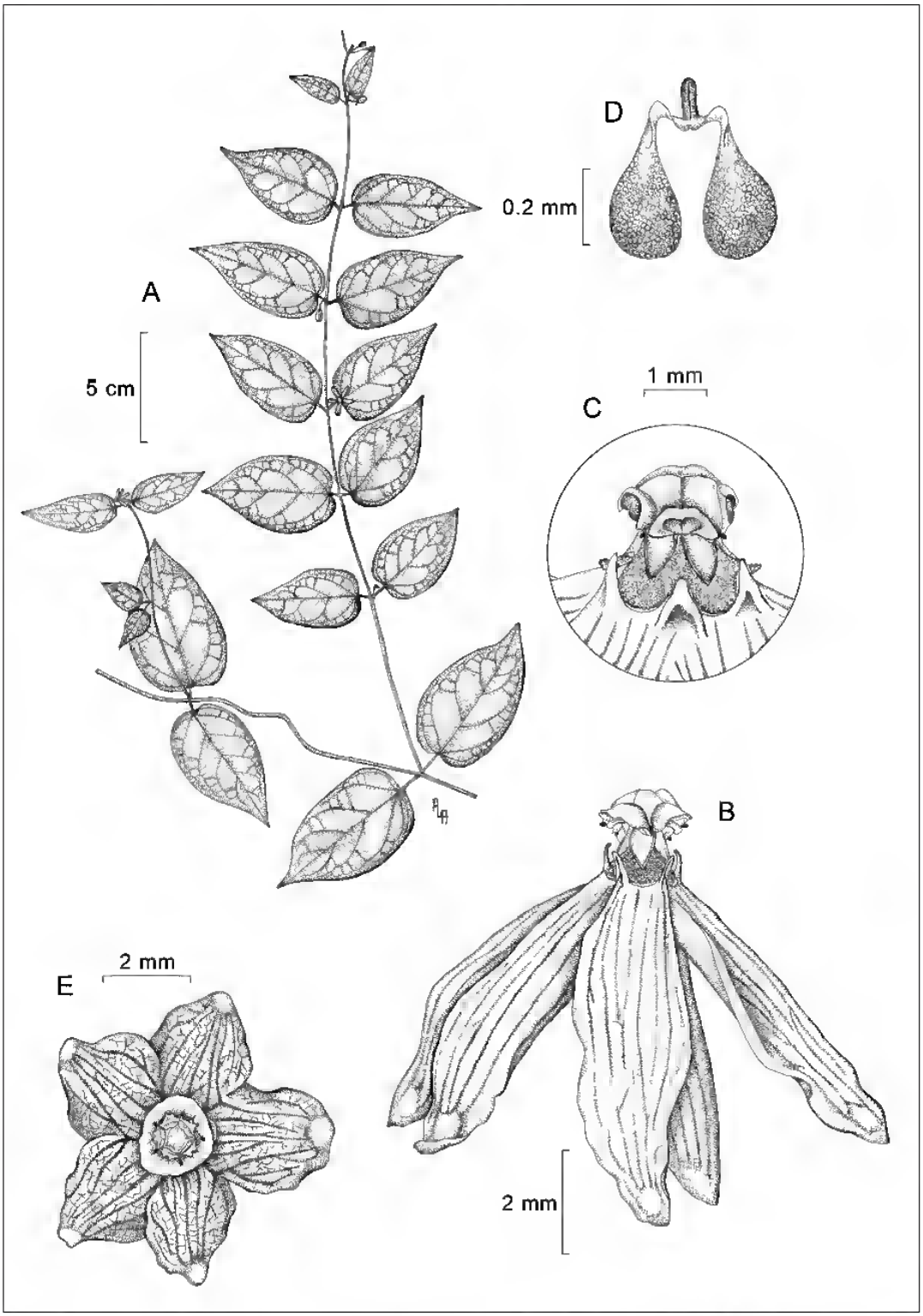

Figure 1. A-D. *Matelea corniculata*. A. Habit. B. Flower. C. Gynostegium. D. Polinarium. E. *Matelea pusilliflora* L.O. Williams. Flower. (A, C-D are illustrated from *Sperry 840*, B is illustrated from *Suazo 238*, E is illustrated from *Contreras 299*, MO)

trichomes. **Inflorescences** racemiform, with dense glandular trichomes, 2- to 4-flowered, peduncle 2–3 mm, bracts linear, 0.5–3 x 0.1–0.5 mm, pedicels 3–5 mm; calyx lobes ovate, 2.1–3.2 x 0.8–1.5 mm, reflexed, glabrous, with 1 colleter within each sinus; corolla apparently brown, reticulate, with a bright white spot at the tip of each lobe, glabrous except with sparse glandular trichomes outside, tube ca. 0.5 mm long, with a horn between each lobe of the corona, this horn erect or slightly curved inward, 0.3–0.4 mm tall, corolla lobes reflexed, elliptic, flat, 6.5–9.2 x 2.5–3.2 mm; gynostegium with a cylindrical stipe 1–1.2 mm tall; corona covering stipe, lobes opposite the anthers, each with a broad, vertically striate, densely papillate margin; anthers generally trapezoidal, terminal appendages conspicuous, appressed to style apex, white, corpusculum sagittate, red-brown, ca. 0.2 x 0.08 mm, translator ca. 0.2 mm, pollinium more or less horizontal, ca. 0.5 x 0.3 mm, obovate, sterile and excavated at base; style apex star-shaped when flattened but strongly convex and nearly circular in outline, in natural form 2–2.1 mm wide. **Follicles and seeds** unknown.

Paratype. **NICARAGUA. Río San Juan.** Mpio. El Castillo: El Guayabo, 11° 1' N, 84° 23' W, 50 m, 7 Jul 2008, *N. Suazo 238* (HULE, MO).

Distribution and ecology. *Matelea cornuculata* is known from two collections, the first from La Selva Biological Station (Heredia, Costa Rica) in 1979 and the second in more or less adjacent Río San Juan, Nicaragua, in 2008, in lowland tropical rainforest. Both collections were flowering in July, in the rainy season. La Selva Biological Station is well protected, but on the other hand it is one of the most intensely studied plots on the earth and the species does not seem to have been recollected in the intervening 35 years. The Nicaraguan collection is more recent, and although the collection locality is now completely deforested, it is adjacent to the relatively well protected Indio-Maiz Biological Reserve and surviving populations may exist. If IUCN standards (IUCN 2001) were applied, this new species would probably fall in the Data Deficient (DD) category.

Our lack of a clear understanding of generic limits of the Gonolobinae is most often blamed on the bizarre floral diversity. Another factor that must be considered is the rarity of many of the species. The five species of ocellate *Matelea* in Mesoamerica are known to us by a total of 18 collections, none with fruits. The single South American species is known by one collection, without fruits, and the five Caribbean species by 34 collections (from Krings, 2011, 2012), with at least immature fruits described for three of the species. The Nicaraguan paratype of *Matelea cornuculata* (2008) is the first collection of an ocellate *Matelea* from Mesoamerica since 1997. Too many species are just too poorly known and likely to become extinct before they are thoroughly described or perhaps even before they are named.

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PROBOSCIDEA FRAGRANS (MARTYNIACEAE) IN EL PASO COUNTY, TEXAS

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ABSTRACT

A recent collection extends the known range of *Proboscidea fragrans* westward in Texas to El Paso County, the northwesternmost station for the species. A distribution map for the species and a key to distinguish it from the other two species of El Paso County are provided.

Proboscidea fragrans is native to Mexico and the southwestern United States (New Mexico and Texas), and has naturalized in Australia, where it is considered a noxious weed (Hevly 1970; Gutierrez 2011). In New Mexico, it is known from one collection from Eddy County (*Pinkava 3146*, ASU). In Texas, it is known from Brewster, Culberson, Jeff Davis, Hudspeth, and Presidio counties. A collection documented here extends the range westward in Texas to El Paso County.

Proboscidea fragrans (Lindl.) Decne. (Martyniaceae), purple devil's claw, toritos, cuernitos.

Voucher specimen. **TEXAS**. El Paso Co.: South corner of intersection between Interstate Highway 10 and Farm-to-Market Road 1110 (Clint exit 42), 31° 35' 57.31" N, 106° 11' 46.25" W, four individuals along FM 1110 at interface between right-of-way and Chihuahuan desert scrub in deep sand deposits (bluepoint association, rolling), growing with *Psorothamnus scoparius*, *Larrea tridentata*, *Boerhavia intermedia*, *Monroa squarrosa*, *Alliona incarnata*, *Portulaca pilosa*, *Pectis papposa* var. *grandis*, *Chamaesyce parryi*, and *Proboscidea althaeifolia*, 26 Sep 2013, *R. Gutierrez, Jr. 3000* with R. Gutierrez, Sr. (BRIT, UTEP).

Turner et al. (2003) mapped this species as occurring in El Paso County, but the author has not seen any specimens to validate this. All specimens at TEX-LL and SRSC used in creating the maps for *Proboscidea formosa* (assumed to mean *P. fragrans*) have been identified by the author as *P. parviflora* (Woot.) Woot. & Standl. or *P. althaeifolia* (Benth.) Decne. Richard Worthington, curator of the UTEP herbarium, also has not seen any specimens of *P. fragrans* from the county (pers. comm.), nor does he include the species in his checklist of the flora of El Paso County (Worthington 1989, 1997). The specimens that are the basis of this paper represent the first vouchered collection of the species in El Paso County. Their presence in El Paso County most likely represent a dispersal event via vehicular transport, given that the plants were found growing immediately next to the right-of-way along FM 1110 and the presence of a series of restaurants, hotels, and gas stations at this exit off of Interstate Highway 10. The closest vouchered collection seen by the author was collected in 1938 from northern Hudspeth County, 15 miles east of the Hueco Mountains (*Hitchcock et al. 4337*, CAS). The next closest collection of *P. fragrans* comes from the far southeastern edge of Hudspeth County, near the Indio Mountains (*Lieb & Anderson 1015*, UTEP)

Proboscidea fragrans has been accepted as a species (Lawrence 1957; Hevly 1970) and as a subspecies of *P. louisianica* (Mill.) Thell. (Bretting 1983). Molecular work using phylogenetic analyses of nuclear and chloroplast sequences fails to place *P. fragrans* as sister to *P. louisianica* (Gutierrez 2002, 2011). Thus, they are recognized here as distinct species.

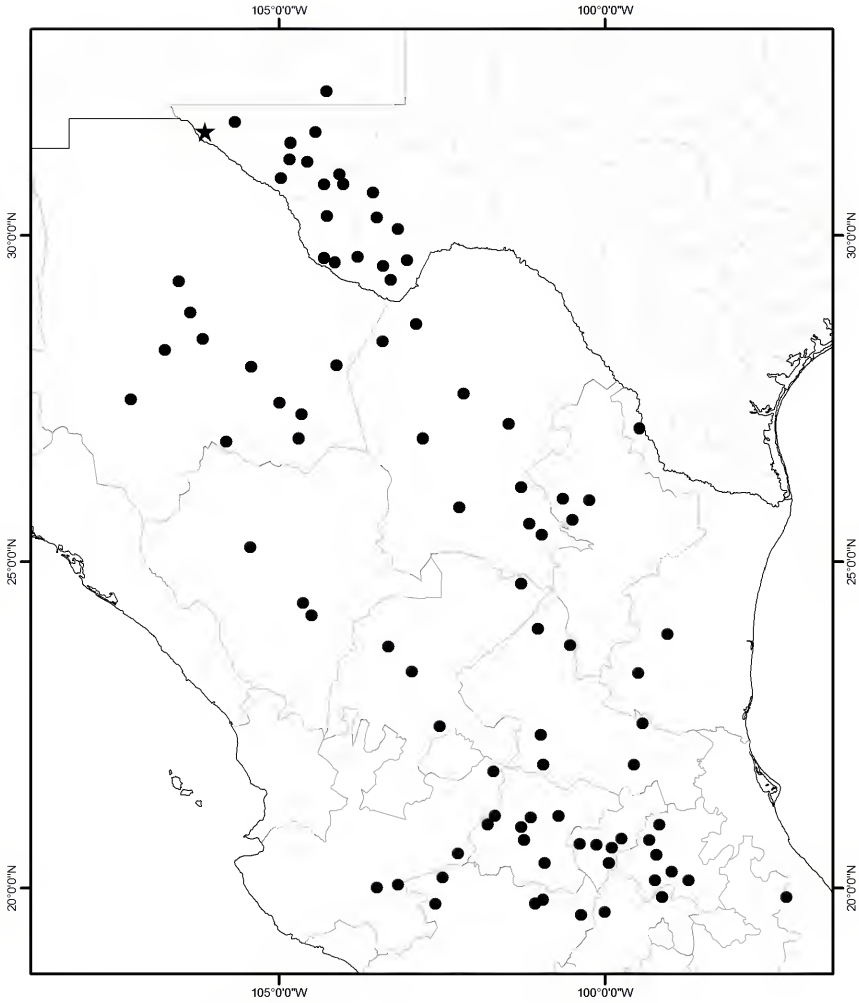

Figure 1. Distribution of *Proboscidea fragrans* (Lindl). Decne. The star represent a new county record for El Paso County, Texas.

Two other species of *Proboscidea* have been documented in El Paso County (Worthington 1989, 1997; Gutierrez 2011). *Proboscidea parivflora* has shorter inflorescences and smaller flowers that are lighter in color. *Proboscidea althaeifolia* is a yellow-flowered perennial with tuberous roots. A key is to the species of *Proboscidea* in El Paso County is provided here.

KEY TO THE SPECIES OF *PROBOSCIDEA* IN EL PASO COUNTY

1. Corollas yellow; plants perennial, arising from an underground tuber; stems trailing or prostrate ..... **Proboscidea althaeifolia**
1. Corollas pink, lavender, purple, or magenta; plants annual, taprooted; stems ascending to erect.
   2. Inflorescences exceeded by or barely exceeding the foliage; flowers fewer than 10 per inflorescence, corollas to 2 cm long, petals pink or lavender ..... **Proboscidea parviflora**
   2. Inflorescences exceeding the foliage; flowers more than 15 per inflorescence, corollas to 4 cm long, petals purple or magenta ..... **Proboscidea fragrans**

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Gutierrez, R., Jr. 2014. Noteworthy collections from Dallas County, Texas. Phytoneuron 2014-56: 1–2. Published 16 June 2014. ISSN 2153 733X

NOTEWORTHY COLLECTIONS FROM DALLAS COUNTY, TEXAS

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The following vascular plant records are a result of collections made in the fall of 2013 in Dallas Co., Texas. Both species were collected from the same locality.

TEXAS. Dallas Co.: Dallas, Cedar Branch Creek at Raleigh Street bridge, 32° 49' 9.29" N, 96° 49' 4.90" W. Associated species at the site include *Ambrosia trifida*, *Ulmus parvifolia*, *Ulmus crassifolia*, *Smilax bona-nox*, *Fraxinus pennsylvanica*, *Bothriochloa ischaemum*, *Calyptocarpus vialis*, *Bacopa monnieri*, *Commelina communis*, and *Cyperus rotundus*. The area was and continues to be frequently mowed and maintained along the sloped banks, though the bed of the creek and the forested areas further back from the sloped banks are left unmaintained. The creek is fed by several culverts which effectively act as the headwaters of Cedar Branch Creek. Directly upstream from this segment of Cedar Branch Creek is the Dallas North Tollway, which very likely provided the seed source for several of the weedy, non-native plants seen at the site.

Malvastrum coromandelianum (L.) Garcke (Malvaceae), three-lobe false mallow

Voucher specimen. 10 Oct 2013, *Gutierrez 2866* (BRIT).

Three-lobe false mallow is a pantropical weed that extends into temperate regions (Correll & Johnston 1979; Diggs et al. 1999). In Texas, it is common from Austin southward to Mexico. Sanchez (1997) also reported the species from Fort Hood, in Bell and Coryell counties. This collection is the furthest north in Texas that the species has been documented (Turner et al. 2003). At this time, the population does not appear to have survived the 2013-2014 winter season, which was the sixth coldest season on record, with 55 days below freezing (National Weather Service 2014).

Mecardonia procumbens (Mill.) Small (Plantaginaceae), prostrate water-hyssop

Voucher specimen. 10 Oct 2013, *Gutierrez 2868* (BRIT).

Prostrate water-hyssop is widespread in Texas though not very common (Correll & Johnston 1979; Diggs et al. 1999). The first known collection from Dallas County was made in 1926 (*Haynes s.n.*, TEX); no other specimens from Dallas County are known. This collection was found growing in the bed of the creek in black clay deposits, and the population appears to have survived the 2013-2014 winter season.

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TYPES OF E.P. BICKNELL'S *SISYRINCHIUM* (IRIDACEAE)

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ABSTRACT

Between 1896 and 1904 Eugene P. Bicknell described and named 78 species of *Sisyrinchium* and its segregate *Hydastylus* (Iridaceae) in the USA, Canada, and Mexico. Though many of these names are surely synonyms, others perhaps represent populations that are not wholly understood and may merit taxonomic recognition. In the absence of a published treatment that addresses these many names, an enumeration is provided that stabilizes Bicknell's names by documentation of their types and, where needed, by designation of appropriate lectotypes or neotypes. Documentation is given for the types of all species of *Sisyrinchium* and *Hydastylus* (Iridaceae) published by E.P. Bicknell. Lectotypes are designated for *Sisyrinchium amoenum*, *S. apiculatum*, *S. arenicola*, *S. asheianum*, *S. atlanticum*, *S. biforme*, *S. bushii*, *S. campestre*, *S. capillare*, *S. corymbosum*, *S. exile*, *S. flagellum*, *S. flexile*, *S. hastile*, *S. helleri*, *S. incrustatum*, *S. intermedium*, *S. macrocarpon*, *S. miamiense*, *S. pruinosum*, *S. radicatum*, *S. rosulatum*, *S. scabrellum*, *S. scoparium*, *S. strictum*, *S. tenellum*, *S. texanum*, *S. tracyi*, *Hydastylus cernuus*, *H. longipes*, and *H. rivularis*. Neotypes are selected for *Sisyrinchium dichotomum*, *S. membranaceum*, and *S. solstitiale*.

In the 1890s a resident of New York City, Eugene Pintard Bicknell (1859–1925), began to record characteristics and differences he had observed in local populations of *Sisyrinchium* (Iridaceae). He was unable to reconcile these observed differences with the then-standard treatments of the eastern USA flora and, though he was only an amateur botanist — his professional interests lay primarily in law and finance — he ventured to put forward his observations in a series of minutely detailed articles, mostly in the widely read Bulletin of the Torrey Botanical Club.

Bicknell's first presentation (1896) was a relatively modest inquiry into the number of "kinds" (the term "taxa" was, of course, yet to be coined) of *Sisyrinchium* to be found in the vicinity of New York City. For a number of years he had observed in Van Cortlandt Park two of these entities that, though similar in structure, were clearly distinct without intergrading forms. Outside the City he found a third entity with even stronger distinguishing characteristics. Though two of the three names he created or applied were incorrect (Ward 1968), he nevertheless brought into focus the characters that have well served to distinguish these three species. [By modern usage, Bicknell's plants are *S. atlanticum* Bicknell, *S. angustifolium* Miller (= *S. graminoides* Bicknell), and *S. montanum* Greene (= *S. angustifolium* Miller, sensu Bicknell).]

Bicknell, then convinced (May 1899) that *Sisyrinchium* was an "extensive *group* of species," undertook a detailed survey of the genus. He attempted to be comprehensive in the USA and Canada, though he gave only limited attention to Mexico. He did this by borrowing the holdings of both individuals and major institutions (apparently, though he was a private citizen, through the auspices of the New York Botanical Garden, whose director, N.L. Britton, had interest in his work), and by developing a widespread network of collectors, which enabled him to build an herbarium of his own. [Bicknell's private collection was given to NY by his widow in 1925.] After what must have been an intensive two years of compilation and study, he began publication of a series of papers, again in the Bulletin of the Torrey Botanical Club. Within the calendar year 1899 he released six papers, totaling

63 pages and reporting 41 new species. He continued this frenetic pace into 1900 with two papers, one documenting the Canadian species, the other reporting an additional 12 species in the segregate *Hydastylus*, which Bicknell recognized at generic level. Still other new species appeared in 1901, 1903, and 1904. Bicknell's preparation of *Sisyrinchium* in Small's compendious Flora of the Southeastern United States (1903) was significant in that only there did he present a key that summarized the differences he believed diagnostic in separating the southeastern species.

In total, Bicknell was responsible for publication of 69 species (and one variety) of *Sisyrinchium* and 9 species of *Hydastylus*. Stability of nomenclature of these perplexing plants will not be reached until a linkage is established between these names and the representative specimens of their natural populations.

Bicknell's contributions to understanding of the genus *Sisyrinchium* were not universally appreciated. A contemporary, the plant anatomist T. Holm, grumpily commented (1908) that he wished to present his own data "before the genus *Sisyrinchium* becomes entirely lost in segregates and in new species, which in late years have accumulated very rapidly ... ." Although Small retained Bicknell's treatment of the genus in the second edition of his Flora of the Southeastern United States (1913), in Small's later, better known Manual of the Southeastern Flora (1933), E.J. Alexander severely edited Bicknell's earlier text, not only deleting many of his species but even omitting mention of them in synonymy.

Bicknell's practice was to cite several, in many cases surely all, of the herbarium materials available to him. These citations generally permit a modern worker to locate the specimen referred to, though the intervening century has seen the dissolution and/or merger of some herbaria or even their destruction (Biltmore, North Carolina). Often Bicknell would note one of the cited collections to be his type, and often he would write "type" on the appropriate sheet (though at times he placed "type" on more than a single sheet of the same collection). Yet all too frequently he made no designation, leaving a later worker to puzzle which of the surviving sheets best fits the diagnosis and be considered the type.

The number of new names in Bicknell's *Sisyrinchium*, coupled with the often subtle morphological distinctions separating species, and compounded by the author's frequently unclear type documentation, has encouraged floristic writers to suppress his names in synonymy rather than attempt linkage between them and the populations they represent. Two regional studies are exceptional: the excellent treatments of *Sisyrinchium* in the Pacific Northwest (Henderson 1976) and the Rocky Mountains (Cholewa & Henderson 1984, 1985) included selection of lectotypes and has greatly assisted in fixing the meaning of certain Bicknell names. Yet many names remain insecure, perhaps listed in synonymy (e.g., Cholewa & Henderson 2002) but with no type formally assigned.

Two unpublished studies merit attention. The first, O'Connell (1955), though his preliminary studies encompassed much of the genus, included in his thesis only those species characterized by unbranched stems. The second, Hornberger (1987), borrowed and annotated a comprehensive volume of herbarium materials but reported she was limited in her field experience to the state of Arkansas and a single brief trip to Louisiana. Regrettably, both of these persons allowed their very informative theses to remain unpublished. Had their graduate dissertations been put in print, they would have encompassed much of the typification and lectotypification attempted here.

Only 30 of Bicknell's new names are now represented by holotypes. More often, either he did not designate any particular collection to be his "type," or where he did so, more than a single specimen, perhaps in different herbaria, are now known. The modern International Code of Botanical Nomenclature (McNeill et al. 2006) provides a formal process for choosing between competing type specimens, by designation of a lectotype. Where no original materials survive, the Code also

provides for selecting a replacement type, a neotype. In the following tabulation, 44 lectotypes are noted, 31 of them newly designated here. And 3 neotypes are selected, where all materials available to Bicknell are believed to no longer exist. Where lectotypes have previously been designated by others (e.g., Henderson 1976; Cholewa & Henderson 1984, 1985), their actions have been noted. The many lectotypes recorded on herbarium labels and in dissertations (O'Connell 1955; Hornberger 1987), though they have no standing under the Code, have been carefully considered and, whenever possible, retained here.

Typification

Entries in the following listing are alphabetical by the epithet. Each provides Bicknell's name, the place and date of its publication, and designation and place of deposit of its type. Where useful, additional notes are appended. It is not believed appropriate in the present format to attempt assignment of all Bicknell names to currently recognized taxa. Judgments differ here and, in the southeastern USA especially, some names may represent populations that are apparent in the field but hidden in synonymy.

Sisyrinchium alpestre E.P. Bicknell in Bull. Torrey Bot. Club 26: 453. Aug 1899. **HOLOTYPE: USA. Colorado**. [Park Co.]: "Meadow, Como," 3 Aug 1895, *Crandall & Cowan 477* (US).

Sisyrinchium amethystinum E.P. Bicknell in Bull. Torrey Bot. Club 28: 581. 1901. **HOLOTYPE: USA. Arizona**. [Pima Co.]: "Rincon Mts.," 1891, *Neally 153* (US).

Sisyrinchium amoenum E.P. Bicknell in Bull. Torrey Bot. Club 28: 584. 1901. **LECTOTYPE** (designated here): **USA. Texas**. [Brazoria Co.]: "[West] Columbia," 1 Apr 1900, *Bush 472* (NY; isolectotype MO). NOTE: If considered synonymous with *S. pruinosum*, the latter name was chosen for the combined taxon by R.L. Oliver (in Correll & Johnston 1970).

Sisyrinchium apiculatum E.P. Bicknell in Bull. Torrey Bot. Club 26: 300. Jun 1899. **LECTOTYPE** (designated here): **USA. Michigan**. [Muskegon Co.]: "Muskegon," Jun 1898, *Beal s.n.* (NY; isolectotype MSC). NOTE: NY collection is on 2 sheets, one (319420) marked "Type" by Bicknell, the second (319421) unmarked.

Sisyrinchium arenicola E.P. Bicknell in Bull. Torrey Bot. Club 26: 496. Sept 1899. **LECTOTYPE** (designated here): **USA. New York**. [Long Island,] "Hempstead," 30 Jun 1899, *Mulford s.n.* (NY). NOTE: Type is chosen from 8 syntypes cited by Bicknell. For nomenclature, see Ward (1968, 1999).

Sisyrinchium asheianum E.P. Bicknell in Bull. Torrey Bot. Club 26: 607. Sept 1899. **LECTOTYPE** (designated here): **USA. North Carolina**. [Rowan Co.]: "Wet meadows, Salisbury," 28 Apr 1897, *Ashe s.n.* (NY; isolectotypes GH, MO, NCU, PH, US). NOTE: Hornberger (1987, in ms.) has suggested the GM specimen as lectotype; but the NY specimen was kept by Bicknell. W.W. Ashe's name is not on the NY label (label reads "Biltmore Herbarium 5751") but is in his hand.

Sisyrinchium atlanticum E.P. Bicknell in Bull. Torrey Bot. Club 23: 134. 1896. **LECTOTYPE** (designated here): **USA. New York**. [Bronx Co.]: "Van Cortlandt Park, New York City," 26 Jun 1891, *Bicknell s.n.* (NY). NOTE: Bicknell cited no specimens in 1896, but referred to plants seen in Van Cortlandt Park and on the New Jersey coast. For nomenclature, see Ward (1968).

Sisyrinchium biforme E.P. Bicknell, Bull. Torrey Bot. Club 28: 575. 1901. **LECTOTYPE** (designated here): **USA. Texas**. [Austin Co.]: "San Felipe," 1835, *Drummond 324* (GH; isolectotype US). NOTE: Type chosen here is in agreement with Hornberger (1987, in ms.).

Hydastylus borealis E.P. Bicknell, Bull. Torrey Bot. Club 27: 378. Jul 1900. **LECTOTYPE** (designated by Cholewa & Henderson, Brittonia 37: 163. 1985): **USA. Washington**. [Whatcom Co.]: "Lake shore," Jul-Aug 1890, *Suksdorf 1004* (WS; isolectotypes GH, MO, UC, WS, WTU). Basionym for *Sisyrinchium boreale* (Bickn.) J.K. Henry, Fl. S. Brit. Columb. 88. 1915. = *Sisyrinchum californicum* (Ker-Gawl.) Ait., Hort. Kew 135. 1812. NOTE: Type chosen from 5 syntypes cited by Bicknell.

Hydastylus brachypus E.P. Bicknell, Bull. Torrey Bot. Club 27: 379. Jul 1900. **LECTOTYPE** (designated by Cholewa & Henderson, Brittonia 37: 163. 1985): **USA. Oregon**. [Lincoln Co.]: "Newport," 1 Jun 1892, *Mulford s.n.* (MO). Basionym for *Sisyrinchum brachypus* (Bicknell) J.K. Henry. = *Sisyrinchum californicum* (Ker-Gawl.) Ait., Hort. Kew 135. 1812. NOTE: Type chosen from 6 syntypes cited by Bicknell.

Sisyrinchium brayi E.P. Bicknell, Bull. Torrey Bot. Club 28: 585. 1901. **HOLOTYPE**: **USA. Texas**. [Galveston Co.]: "Flat coastal prairie, Virginia Point, opposite Galveston," 20 Apr 1899, *Bray s.n.* (NY). NOTE: If considered synonymous with *S. pruinosum*, the latter name was chosen for the combined taxon by R.L. Oliver (in Correll & Johnston, 1970).

Sisyrinchium bushii E.P. Bicknell, Bull. Torrey Bot. Club 28: 587. 1901. **LECTOTYPE** (designated here): **USA. Oklahoma**. [Creek Co.]: "Sapulpa, Indian Territory," 20 Apr 1895, *Bush 971* (NY; isolectotypes MO, US). NOTE: If considered synonymous with *S. pruinosum*, the latter name was chosen for the combined taxon by R.L. Oliver (in Correll & Johnston, 1970).

Sisyrinchium campestre E.P. Bicknell, Bull. Torrey Bot. Club 26: 341. Jul 1899. **LECTOTYPE** (designated here): **USA. Missouri**. [Atchison Co.]: "Atchison," 7 Jun 1894, *Bush 682* (MO). NOTE: Type chosen from 28 syntypes cited by Bicknell, in agreement with manuscript selections of O'Connell (1955) and Hornberger (1987).

Sisyrinchium campestre var. ***kansanum*** E.P. Bicknell, Bull. Torrey Bot. Club 26: 344. Jul 1899. **HOLOTYPE**: **USA. Kansas**. [Davis Co.]: "Ft. Riley," 27 Apr 1892, *Norton 514* (NY). Basionym for *Sisyrinchum kansanum* (Bickn.) Alexander, New Britt. & Br. Illust. Fl. 1: 451. 1952. NOTE: Bicknell also cited 5 paratypes.

Sisyrinchium canbyi E.P. Bicknell, Bull. Torrey Bot. Club 28: 588. 1901. **HOLOTYPE**: **USA. Texas**. [Brazoria Co.]: "[West] Columbia," 25 Mar 1900, *Canby 238* (NY). NOTE: *Canby 237* (GH) is of same date and location

Sisyrinchium capillare E.P. Bicknell, Bull. Torrey Bot. Club 26: 608. Dec 1899. **LECTOTYPE** (designated here): **USA. South Carolina**. [Aiken Co.]: "Aiken," May 1899, *Ashe s.n.* (NY-319439). NOTE: Bicknell cited 5 collections of the species, all by W.W. Ashe, all in April or May 1899. Label data indicated the 2 from Florida were collected in "flat woods," 13 May, "20 mi. s. Jacksonville" (thus apparently Clay Co.), and 18 May, "14 mi. s.e. Jacksonville" (thus surely St. Johns Co.). In the same month of 1899 Ashe made other collections (including the type designated here) in western South Carolina (Aiken) where the species is frequent and in Georgia. Hornberger (1987, in ms.) has proposed typifying *S. capillare* with the Florida specimen of 13 May. But the species has never again been found in n.e. Florida (incl. Duval, Clay, and St. Johns cos.), and it is unlikely that Ashe could have found it twice in separate Florida locations. The probability is high that Ashe's Florida labels reflect confused data. The type designated here is unambiguous.

Sisyrinchium carolinianum E.P. Bicknell, Bull. Torrey Bot. Club 26: 221. May 1899. **HOLOTYPE**: **USA. South Carolina**. [Anderson Co.]: "Andersonville," 1886, *Gibbes s.n.* (NY). NOTE: name is legitimate; see *S. fibrosum*.

Hydastylus cernuus E.P. Bicknell, Bull. Torrey Bot. Club 27: 384. Jul 1900. **LECTOTYPE** (designated here): **MEXICO. Chihuahua**. "High plains between Cusihuiriachic and Guerrero," 7 Sep 1887, *Pringle 1376* (NY; isolectotypes BR, GH, MIN, NDG, US). Basionym for *Sisyrinchum cernuum* (Bicknell) Kearney, Leafl. W. Bot. 5: 197. 1949. NOTE Type chosen from 2 syntypes cited by Bicknell.

Sisyrinchium colubriferum E.P. Bicknell, Bull. Torrey Bot. Club 28: 589. 1901. **HOLOTYPE**: **USA. Texas**. [Brazoria Co.]: "Common on prairie, [West] Columbia," 9 April 1899, *Bush 66* (NY; isotype MO). NOTE: If considered synonymous with *S. prunosum*, the latter name was chosen for the combined taxon by R.L. Oliver (in Correll & Johnston, 1970).

Sisyrinchium corymbosum E.P. Bicknell, Bull. Torrey Bot. Club 26: 218. May 1899. **LECTOTYPE** (designated here): **USA. Florida**. [Duval Co.]: "Pine barrens near Jacksonville," 1 Jun 1894, *Curtiss 4584* (US-92713; isolectotypes MO, NY, US). Syntype: **USA**. Alabama, Mobile Co.]: "damp grassy banks, Mobile," 5 Apr 1897, *Mohr s.n.* NOTE The US specimens (two plants on same sheet) are marked "Type" in Bicknell's hand. The NY specimen was marked by Bicknell "part of type but very untypical." Query: Can a type be "untypical"?

Sisyrinchium dichotomum E.P. Bicknell, Bull. Torrey Bot. Club 26: 609. Dec 1899. **NEOTYPE** (selected here): **USA. North Carolina**. [Rutherford Co.]: "Sugarloaf Mountain, flowers white," 25 Jul 1933, *Grover s.n.* (TENN). NOTE Neotype is chosen in agreement with that selected by Hornberger (1987, in ms.). The holotype (Rutherford Co., Chimney Rock, 11 May 1899, *Ashe*?) is lost, presumably with destruction of the Biltmore Herbarium, Asheville, NC.

Sisyrinchium eastwoodiae E.P. Bicknell, Bull. Torrey Bot. Club 31: 385. 1904. **HOLOTYPE**: **USA. California**. [San Bernadino Co.]: "In meadows, San Bernadino Valley," May 1886, *Parish 663* (NY; isotypes BR, MO). NOTE Bicknell (1904) also cited 8 paratypes, from Kern Co. (*Greene*, in 1889; *Eastwood*, in 1894), from San Bernadino Co. (*Parish*, in 1880, 1888, 1889, 1894), and from San Diego Co. (*Henshaw*, in 1803; *Palmer* 1875), all now presumed NY.

Sisyrinchium ensigerum E.P. Bicknell, Bull. Torrey Bot. Club 28: 580. 1901. **HOLOTYPE**: **USA. Texas**. [Bexar Co.]: "San Antonio," 1884, *Jermy s.n.* (US-92716; isotype US).

Sisyrinchium exile E.P. Bicknell, Bull. Torrey Bot. Club 28: 573. 1901. **LECTOTYPE** (designated here): **USA. Texas**. [Galveston Co.]: "Sandy sea shores at Galveston," 25 Feb 1890, *Bodin 73* (US; isolectotype MIN). NOTE Bicknell (1901) cited 2 duplicates. The present selection is the reverse of that of Hornberger (1987, in ms.).

Sisyrinchium farwellii E.P. Bicknell, Bull. Torrey Bot. Club 26: 298. Jun 1899. **LECTOTYPE** (designated by Ward, Taxon 48: 584. 1999): **USA. Michigan**. [Oakland Co.]: "Birmingham," 27 Sep 1898, *Farwell 1625* (NY; isolectotypes BLH, GH, MSC). NOTE Alexander (in Gleason, 1952) treated *S. farwellii* as a form of *S. atlanticum*. Voss (1966, 1972), noting priority of the name over *S. arenicola*, retained *S. farwellii* as unique to the type collection. Type was annotated by Cholewa & Henderson in 1994 as "*Sisyrinchum fuscatum* Bicknell;" this use was accepted by Gleason & Cronquist (1991), Cholewa & Henderson (2002), and Voss & Reznicek (2012).

Sisyrinchium fibrosum E.P. Bicknell, Small, Fl. S.E. U.S. ed. 1, 298. 1903. Nom. succed.: *S. carolinianum* Bicknell (1899). NOTE: Bicknell (in Small 1903) proposed this name as substitute for *S. carolinianum* Bickn., a presumed later homonym of *S. carolinianum* Klotzsch ex Klatt (1861). But Klatt was merely citing in synonymy a herbarium name used by Klotzsch; Klatt's name was not validly published, thus poses no impediment to *S. carolinianum*.

Sisyrinchium flaccidum E.P. Bicknell, Bull. Torrey Bot. Club 28: 591. 1901. **HOLOTYPE**: **USA. Texas**. [Brazoria Co.]: "[West] Columbia," 6-7 Apr 1899, *Bush 466* (NY; isotypes MO, US). NOTE: Bicknell (1901) cited 3 syntypes.

Sisyrinchium flagellum E.P. Bicknell, Bull. Torrey Bot. Club 26: 226. May 1899. **LECTOTYPE** (designated here): **USA. Florida**. [Monroe Co.]: "[Big] Pine Key," pre 1853, *Blodgett s.n.* (NY). NOTE: *S. flagellum* was previously lectotypified (Ward 1999) by a Manatee Co. specimen (*Rothrock*, NY), in error. The Manatee Co. plant has coarse leaves, in serious conflict with Bicknell's description (0.5-1.5 mm. wide). Art. 9.17(b) permits the correction. If considered synonymous with *S. miamiense*, the latter name was chosen for the combined taxon by Ward (1976).

Sisyrinchium flaviflorum E.P. Bicknell, Bull. Torrey Bot. Club 26: 345. Jul 1899. **HOLOTYPE**: **USA. Missouri**. [Jackson Co.]: "Courtney," 7 Jun 1892, *Bush s.n.* (MO).

Sisyrinchium flexile E.P. Bicknell, Bull. Torrey Bot. Club 26: 613. Dec 1899. **LECTOTYPE** (designated here): **USA. Mississippi**. [Jackson Co.]: "Petit Bois Island," 8 May 1898, *Tracy 4469* (NY; isolectotype US). NOTE: This typification confirms choice made by Hornberger (1987, in ms.). She termed the NY specimen to be "holotype," but neither specimen was marked as type by Bicknell.

Sisyrinchium floridanum E.P. Bicknell, Bull. Torrey Bot. Club 26: 222. May 1899. **HOLOTYPE**: **USA. Florida**. [Lake Co.]: "Dry sandy hillside, Lake Dot, Eustis," 12 Mar 1894, *Nash 13* (NY; isotypes BH, GH, MICH, MO, NDG, NY, US). Nom. illeg.: non *S. floridanum* Raf (1840). Nom. succed.: *Sisyrinchium bicknellianum* M.L. Fernald (Rhodora 46: 43. 1944). NOTE: Isotypes are per Hornberger (1987, in ms.).

Sisyrinchium furcatum E.P. Bicknell, Bull. Torrey Bot. Club 26: 229. May 1899. **HOLOTYPE**: **USA. Louisiana**. [Tangipahoa Par.]: "Pine lands, Hammond," 4 Apr 1989, *Gallup 18* (US).

Sisyrinchium fuscatum E.P. Bicknell, Bull. Torrey Bot. Club 26: 225. May 1899. **LECTOTYPE** (designated by Ward, Taxon 48: 583. 1999): **USA. Alabama**. [Escambia Co.]: "Flomaton," 23 Apr 1898, *Baker 1493* (NY; isolectotype US). NOTE: Selected from 4 syntypes. If considered synonymous with *S. nashii*, the latter name was chosen for the combined taxon by Wunderlin (1985).

Sisyrinchium graminoides E.P. Bicknell, Bull. Torrey Bot. Club 23: 133. 1896. Nom. nov.: *S. gramineum* Curtis (1799), non Lam. (1783); *S. bermudiana* auth., non L. (1753); *S. anceps* Watson (1890), non Cav. (1788). Nom. succed.: *Sisyrinchium angustifolium* Mill. (1768). NOTE: For nomenclature, see Ward (1968).

Sisyrinchium greenei E.P. Bicknell, Bull. Torrey Bot. Club 31: 383. 1904. **HOLOTYPE**: **USA. California**. [Siskiyou Co.]: "North side of Mount Shasta," 11-16 Jun 1897, *Brown 351* (NY; isotypes CAS, MIN, MO, US).

Sisyrinchium hastile E.P. Bicknell, Bull. Torrey Bot. Club 26: 297. Jun 1899. **LECTOTYPE** (designated here): **USA. Michigan**. [Wayne Co.]: "Sandy shores of Belle Isle in Detroit River," 2 Jun 1896, *Farwell 867* (NY; isolectotypes BLH, GH). NOTE: A species of unknown affinities, perhaps of horticultural origin. E.J. Alexander in Gleason (1952) identified it as *S. jucundum* E. Meyer, from S. America.; Voss (1972) observed it did not quite match that species and tentatively referred it to *S. pringlei* Robins. & Greenm. of Mexico. [The plant of horticulture is probably *S. junciformum* Herb., of Chile (Dress 1976).] Bicknell had noted "spathes in a conjugate pair," a trait of *S. albidum*, a Michigan native. But he also reported "partly free filaments," a trait not found in any native northeast *Sisyrinchium*. Hornberger (1987, in ms.) placed the name in synonymy of both *S. albidum* Raf. (p. 89) and *S. mucronatum* Michx. (p. 179), without comment. Voss and Reznicek (2012) suggested it be referred to *S. capillare* Bickn., a species also with paired spathes (but with wholly-connate filaments), native to the coastal Southeast (Virginia to Georgia).

Sisyrinchium helleri E.P. Bicknell, Bull. Torrey Bot. Club 28: 590. 1901. **LECTOTYPE** (designated here): **USA. Texas**. [Nueces Co.]: "Along Corpus Christi bay," 9-12 April 1894, *Heller 1552* (NY; isolectotype US). NOTE: If considered synonymous with *S. pruinosum*, the latter name was chosen for the combined taxon by R.L. Oliver (in Correll & Johnston, 1970).

Sisyrinchium hesperium E.P. Bicknell, Bull. Torrey Bot. Club 31: 390. 1904. **HOLOTYPE: USA. California**. [Santa Barbara Co.?]: "Dutard's Ranch, near the boundary between Santa Barbara and San Luis Obispo counties," 9 May 1896, *Eastwood s.n.* (CAS).

Sisyrinchium heterocarpum E.P. Bicknell, Bull. Torrey Bot. Club 26: 348. Jul 1899. **LECTOTYPE** (designated by Cholewa & Henderson, Brittonia 36: 358. 1984): **USA. Wyoming**. [Goshen Co.]: "Table Mountain," 30 Jun 1895, *Nelson 1390* (MO; isolectotypes MIN, NY, WIS). NOTE: Bicknell cited 3 syntypes.

Sisyrinchium idahoense E.P. Bicknell, Bull. Torrey Bot. Club 26: 445. Aug 1899. **LECTOTYPE** (designated by Henderson, Brittonia 28: 175. 1976): **USA. Idaho**. [Nez Perce Co.]: "Valley of Big Potlatch River," 6 Jun 1892, *Sandberg 317*. (US; isolectotype NY). NOTE: Of 10 collections cited by Bicknell, none was designated as type. Though Henderson (1976) has stated the US specimen to be the holotype, it is better to consider his designation as lectotype. If considered synonymous with *S. occidentale*, the present name was chosen for the combined taxon by Henderson (1976).

Sisyrinchium implicatum E.P. Bicknell, Bull. Torrey Bot. Club 26: 228. May 1899. **HOLOTYPE: USA. Mississippi**. [Calhoun Co.]: "Wet bottoms," Apr 1858, *Hilgard s.n.* (MO).

Sisyrinchium incrustatum E.P. Bicknell, Bull. Torrey Bot. Club 26: 606. Dec 1899. **LECTOTYPE** (designated here): **USA. North Carolina**. [Forsythe Co.]: "Open grassy wooded hillside, near Winston," Jul 1897, *Ashe 2257* (NCU). NOTE: Type chosen from 3 syntypes cited by Bicknell.

Sisyrinchium intermedium E.P. Bicknell, Bull. Torrey Bot. Club 26: 498. Sept 1899. **LECTOTYPE** (designated here): **USA. North Carolina**. [Buncombe Co.]: "Open woodlands, Biltmore," 8 May 1897, *Ashe s.n.* (GH; isolectotypes MO, NCSC, NCU, NY, PH). NOTE: Type chosen from 10 syntypes cited by Bicknell, in agreement with selection by Hornberger (1987, ms.). Printed label reads "Biltmore Herbarium 4602b." But collector/correspondent was surely W.W. Ashe.

Sisyrinchium leptocaulon E.P. Bicknell, Bull. Torrey Bot. Club 26: 451. Aug 1899. **LECTOTYPE** (designated by Henderson, Brittonia 28: 167. 1976): **USA. Nevada**. [Elko Co.]: "Deeth," 14 Jul 1896, *Greene s.n.* (NY; isolectotype NDG).

Sisyrinchium longifolium E.P. Bicknell, Small, Fl. S.E. U.S. ed. 1, 300, 1329. 1903. Nom. illeg., non *S. longifolium* Phil. (1895). **HOLOTYPE: USA. Florida**. [Manatee Co.]: "Manatee," 8 May 1900, *Tracy 6672* (NY). NOTE: Second collection from same location (7 May 1900, *Tracy 6673*) marked by Bicknell as "very unlike type." Hornberger (1986 annot.): *Tracy 6672* is *S. atlanticum*, *Tracy 6673* is *S. nashii*.

Sisyrinchium longipedunculatum E.P. Bicknell, Bull. Torrey Bot. Club 28: 577. 1901. **HOLOTYPE: USA. Texas**. [Culberson Co.]: "On top of Guadaloupe Mountains," Oct 1881, *Havard s.n.* (US).

Hydastylus longipes E.P. Bicknell, Bull. Torrey Bot. Club 27: 382. Jul 1900. **LECTOTYPE** (designated here): **USA. Arizona**. [Coconino Co.]: "San Francisco mountain," 18 Aug 1889, *Knowlton 34* (NY, not confirmed; US). Basionym for *Sisyrinchium longipes* (Bicknell) Kearney & Peebles, Wash. Acad. Sci. 29:474. 1939. NOTE: Type chosen from 5 syntypes cited by Bicknell. A different syntype, *Townsend 69* (NDG), from Chihuahua, Mexico, has been proposed by B. Hellenthal (annot. on sheet, Aug 2013).

Sisyrinchium macounii E.P. Bicknell, Bull. Torrey Bot. Club 27: 245. May 1900. **LECTOTYPE** (designated by Henderson, Brittonia 28: 172. 1976): **CANADA. British Columbia**. [Vancouver Island], "meadows, Comox," 21 Jun 1893, *Macoun 4393* (CAN; isolectotype GH). Henderson used "holotype" in reference to the CAN specimen, corrected here.

Sisyrinchium macrocarpon E.P. Bicknell, Bull. Torrey Bot. Club 28: 576. 1901. **LECTOTYPE** (designated here): **USA. Arizona**. [Coconino Co.]: "Willow Springs," 10-20 Jun 1890, *Palmer 490a* (US; isolectotype GH).

Sisyrinchium membranaceum E.P. Bicknell, Bull. Torrey Bot. Club 26: 612. Dec 1899. **NEOTYPE** (selected here): **USA. Florida**. [Jackson Co.]: "4.7 mi. n. of Marianna; many plants observed, all with white perianths," 22 Apr 1987, *Godfrey 82351* (FLAS; isoneotype FSU); det. as *S. angustifolium* Mill., by M. Drummond. NOTE: The holotype (Florida, Jackson Co., Marianna, 20 Apr 1899, *Ashe?*) is now lost, presumably with destruction of the Biltmore Herbarium, Asheville, NC. Spm. selected here is geographically correct. But Bicknell's description does not fully match any known Florida *Sisyrinchium* (fls. described as "violet-blue," etc.).

Sisyrinchium miamiense E.P. Bicknell, Bull. Torrey Bot. Club 26: 226. May 1899. **LECTOTYPE** (designated here): **USA. Florida**. [Dade Co.]: "Miami," 4-7 Apr 1898, *Pollard & Collins 264* (NY; isolectotypes MIN, NDG, US). NOTE: Photo of type: Ward (1976).

Sisyrinchium nanum E.P. Bicknell, Bull. Torrey Bot. Club 26: 615. Dec 1899. **HOLOTYPE: USA. Mississippi**. [Jackson Co.]: "Horn Island," 1 Jun 1898, *Tracy 5346* (NY). Nom. illeg., non *S. nanum* Phil. (1895).

Sisyrinchium nashii E.P. Bicknell, Bull. Torrey Bot. Club 26: 223. May 1899. **LECTOTYPE** (designated by Ward, Taxon 48: 583. 1999): **USA. Florida**. [Lake Co.]: "Dry sandy soil of low pine land region, Lake Swatara, Eustis," 24 Jul 1894, *Nash 1395* (NY; isolectotypes GH, MICH, MIN, US). NOTE: Type chosen from 2 syntypes cited by Bicknell.

Sisyrinchium occidentale E.P. Bicknell, Bull. Torrey Bot. Club 26: 447. Aug 1899. **LECTOTYPE** (designated by Henderson, Brittonia 28: 174. 1976): **USA. Idaho**. [Butte Co.]: "Arco," 18 Jun

1893, *Palmer 165* (US; isolectotypes MICH, WIS). NOTE: The specimen chosen by Henderson is one of 17 syntypes cited by Bicknell.

Sisyrinchium oreophilum E.P. Bicknell, Bull. Torrey Bot. Club 31: 381. 1904. **HOLOTYPE: USA. California**. [Mariposa Co.]: "Yosemite Valley," May-Jun 1900, *Bioletti s.n.* (CAS).

Hydastylus parvus E.P. Bicknell, Bull. Torrey Bot. Club 27: 384. Jul 1900. **HOLOTYPE: MEXICO. Coahuila**. "Low valley near Saltillo," 22 Mar 1847, *Gregg 340* (MO). [*Sisyrinchium parvum* (Bickn.) ined.] = *Sisyrinchium schaffneri* Watson.

Sisyrinchium pruinosum E.P. Bicknell, Bull. Torrey Bot. Club 28: 578. 1901. **LECTOTYPE** (designated here): **USA. Texas**. [Dallas Co.]: "Common in woods, Dallas," 13 Apr 1900, *Bush 561* (NY; isolectotype MO). NOTE: Type chosen from 2 syntypes. Type not designated by Bicknell in publication of the species, but written on herbarium label.

Sisyrinchium radicatum E.P. Bicknell, Bull. Torrey Bot. Club 28: 576. 1901. **LECTOTYPE** (designated here): **USA. Utah**. [Washington Co.]: "St. George," 1877, *Palmer 456* (NY; isolectotypes GH, ISC).

Sisyrinchium recurvatum E.P. Bicknell, Small, Fl. S.E. U.S. ed. 1, 299, 1329. 1903. **HOLOTYPE** (designated by Bicknell in Small): **USA. Florida**. [Manatee Co.]: "In sand, Longboat Key," May 1900, *Tracy 6675* (NY; isotype NY).

Hydastylus rivularis E.P. Bicknell, Bull. Torrey Bot. Club 27: 381. Jul 1900. **LECTOTYPE** (designated here): **USA. California**. [Fresno Co.]: "Ford of Bubb's Creek," 5 Jul 1899, *Eastwood s.n.* (NY; isolectotype NDG). = *Sisyrinchium elmeri* Greene, Pittonia 2: 106. 1890. NOTE: Type chosen from 3 syntypes cited by Bicknell.

Sisyrinchium rosulatum E.P. Bicknell, Bull. Torrey Bot. Club 26: 228. May 1899. **LECTOTYPE** (designated here): **USA. South Carolina**. [Charleston Co.]: "Sullivan's Island," 8 May 1852, *Gibbes s.n.* (NY). NOTE: Type chosen from 2 syntypes cited by Bicknell.

Sisyrinchium rufipes E.P. Bicknell, Bull. Torrey Bot. Club 26: 224. May 1899. **HOLOTYPE: USA. Georgia**. [Richmond Co.]: "Dry sand hills, Augusta," 24 Mar [1899], *Cuthbert s.n.* (NY). NOTE: If considered synonymous with *S. fuscatum*, the latter name was chosen for the combined taxon by Cholewa and Henderson (2002).

Sisyrinchium sagittiferum E.P. Bicknell, Bull. Torrey Bot. Club 26: 230. May 1899. **HOLOTYPE: USA. Texas**. [Bastrop Co.]: "On sand bars in the Colorado [River], opposite Bastrop," 1 May 1839, *Riddell s.n.* (NY).

Sisyrinchium scabrellum E.P. Bicknell, Bull. Torrey Bot. Club 26: 230. May 1899. **LECTOTYPE** (designated here): **USA. North Carolina**. [Buncombe Co.]: "Near Biltmore," 10 May 1898, *Biltmore Herbarium 5752b* (NSC; isolectotypes MO, NY, US). NOTE: Type chosen from 2 syntypes cited by Bicknell. Type chosen is in agreement with O'Connell (1955, in ms.) and Hornberger (1987, in ms.).

Sisyrinchium scoparium E.P. Bicknell, Bull. Torrey Bot. Club 26: 227. May 1899. **LECTOTYPE** (designated here): **USA. Mississippi**. [Harrison Co.]: "Biloxi," 27 Apr 1898, *Baker 1496* (NY). NOTE: Bicknell stated type was in herbarium of Alabama Biol. Survey (present location unknown, perhaps lost by destruction of the Auburn Univ. herbarium, by fire); but his description must have been drawn from the specimen selected here, a duplicate. Bicknell cited one paratype, also from Biloxi: *Tracy* (NY).

Sisyrinchium segetum E.P. Bicknell, Bull. Torrey Bot. Club 26: 449. Aug 1899. **LECTOTYPE** (designated by Henderson, Brittonia 28: 174. 1976): **USA. Washington**. [King Co.]: "In full flower, Seattle," May 1892, *Piper s.n.* (NY; isolectotypes GH, US). NOTE: Bicknell cited 5 syntypes. If considered synonymous with *S. occidentale*, the latter name was chosen for the combined taxon by Henderson (1976).

Sisyrinchium septentrionale E.P. Bicknell, Bull. Torrey Bot. Club 26: 452. Aug 1899. **LECTOTYPE** (designated by Henderson, Brittonia 28: 166. 1976): **CANADA. Alberta**. "National Park, near Banff," 8 Jul 1891, *Macoun 4392* (MO; isolectotypes GH, NY, US). NOTE: Bicknell cited 3 syntypes.

Hydastylus serrulatus E.P. Bicknell, Bull. Torrey Bot. Club 27: 385. Jul 1900. **HOLOTYPE**: **MEXICO. Veracruz**. "In the mountains, Orizaba," (date?), *Botteri 1856* (ALU, not confirmed). Basionym for: *Sisyrinchium serrulatum* (Bickn.) Espe & Lopez-Ferr., Acta Bot. Mex. 41:4. 1997.

Sisyrinchium solstitiale E.P. Bicknell, Bull. Torrey Bot. Club 26: 219. May 1899. **NEOTYPE** (selected here): **USA. Florida**. [Lake Co.]: "Dry sandy soil, Eustis," 20 Mar 1894, *Nash 133* (NDG; isoneotypes BH, GH, MIN, MO, NY, US). NOTE: The specimen designated as type by Bicknell (Lake Co.: "High pine land, Eustis," 10 Aug 1894, *Nash s.n.*), then in the private herbarium of G.V. Nash, is now lost, presumably in the destruction of the Biltmore Herbarium, Asheville, NC. Hornberger (1987, in ms.) suggested a 1901 collection from Dade Co. (*Small & Nash 272* - NY) as neotype. However, neotype chosen here is by same collector and location/year as lost original, and is widely distributed. This collection is also the type of *X. xerophyllum* Greene (Mar 1899), thus establishing unequivocal synonymy.

Sisyrinchium strictum E.P. Bicknell, Bull. Torrey Bot. Club 26: 299. Jun 1899. **LECTOTYPE** (designated here): **USA. Michigan**. [Montcalm Co.]: "Vestaburg," 22 Jun 1898, *Wheeler s.n.* (NY, 2 sheets; isolectotype MICH). NOTE: Voss (1967, 1972) early identified the specimens used by Bicknell, but did not select either as type (he did call MICH an "apparent isotype"); this omission remedied here.

Sisyrinchium subcernuum E.P. Bicknell, Bull. Torrey Bot. Club 27: 385. Jul 1900. **HOLOTYPE** (designated by Bicknell): **MEXICO. Baja California Sur**. "Sierra de la Laguna," 22 Jan [1899], *Brandegee s.n.* (CAS). Basionym for *Hydastylus subcernuus* (Bickn.) J.E. Henrich & P. Goldblatt, Ann. Missouri Bot. Gard. 74: 908. 1988.

Sisyrinchium tenellum E.P. Bicknell, Bull. Torrey Bot. Club 26: 610. Dec 1899. **LECTOTYPE** (designated here): **USA. Alabama**. [Lee Co.]: "Auburn," 9 May 1896, *Earle s.n.* (NY, 2 sheets). NOTE: Type chosen from 5 syntypes cited by Bicknell. Type chosen here is in agreement with Hornberger (1987, in ms.).

Sisyrinchium texanum E.P. Bicknell, Bull. Torrey Bot. Club 28: 578. 1901. **LECTOTYPE** (designated here): **USA. Texas**. [Harris Co.]: "Houston," 12 Apr 1972, *Hall 636* (NY, 2 sheets; isolectotypes GH, MO, US). NOTE: Type chosen from 3 syntypes cited by Bicknell.

Sisyrinchium tortum E.P. Bicknell, Bull. Torrey Bot. Club 26: 221. May 1899. **LECTOTYPE** (designated by Ward, Taxon 48: 583. 1999): **USA. Mississippi**. [Harrison Co.]: "Biloxi," 20 Mar 1898, *Tracy 4460* (NY; isolectotype PH). NOTE: Type chosen from 2 syntypes cited by Bicknell.

Sisyrinchium tracyi E.P. Bicknell, Bull. Torrey Bot. Club 26: 614. Dec 1899. **LECTOTYPE** (designated here): **USA. Mississippi**. [Harrison Co.]: "Biloxi, Point San Martin," 20 Mar 1898, *Tracy 4459* (NY; isolectotypes NCU, US).

Hydastylus translucens E.P. Bicknell, Bull. Torrey Bot. Club 27: 386. Jul 1900. **HOLOTYPE**: **MEXICO. Baja California Sur**. "Sierra de la Laguna," 24 Jan [1899], *Brandegee s.n.* (CAS). Basionym for *Sisyrinchium translucens* (Bickn.) Espejo & Lopez-Ferr., Acta Bot. Mex. 41: 5. 1997.

Sisyrinchium varians E.P. Bicknell, Bull. Torrey Bot. Club 28: 583. 1901. **HOLOTYPE**: **USA. Texas**. [Travis Co.]: "Austin," Mar 1870, *Bodin s.n.* (US). NOTE: Bicknell cited 5 paratypes. If considered synonymous with *S. pruinosum*, the latter name was chosen for the combined taxon by R.L. Oliver (in Correll & Johnston 1970).

Sisyrinchium versicolor E.P. Bicknell, Bull. Torrey Bot. Club 26: 606. Dec 1899. **HOLOTYPE**: **USA. Michigan**. [Wake Co.]: "Hillsides, Raleigh," May 1896, *Ashe 336* (NCU). NOTE: Bicknell also cited 5 paratypes.

Sisyrinchium violaceum E.P. Bicknell, Small, Fl. S.E. U.S. 301, 1329. 1903. **HOLOTYPE**: **USA. Florida**. "Walton Co.," summer 1885, *Curtiss s.n.* (NY).

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PUCCINELLIA PARISHII (POACEAE, POEAE): A GENUS AND SPECIES NEW TO TEXAS

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ABSTRACT

Puccinellia parishii is reported as a genus and species new to Texas. The species is here reported from the Chinati Mountains of Presidio County in the Trans-Pecos region of West Texas, greatly extending eastward the previously recorded distribution of the species. The species was previously known from about 30 locales in California, Arizona, New Mexico, Utah, and Colorado. At one time *P. parishii* was proposed for listing as an endangered species, but was removed from the candidate list because of abundance. The species is globally ranked G2G3 (imperiled and very vulnerable to extinction throughout its range) but is ranked S1 (critically imperiled) in Texas.

Puccinellia, commonly known as alkali grass, is a genus found in saline or alkaline environments in the subtropics to Arctic regions of the Northern Hemisphere. With the exception of the southeastern USA and Hawaii, the genus has been reported throughout the USA and Canada. *Puccinellia parishii,* commonly known as Parish's alkali grass or bog alkali grass, occurs in continuously moist alkaline desert springs, or cienegas. This species has been reported from about 30 sites in New Mexico, Arizona, California, Utah, and Colorado (Davis & Consaul 2007; SEINET 2014; BONAP 2014; Colorado Natural Heritage Program 1997+). Here we report the genus and species as the first alkali grass in the state.

Voucher. **Texas**. Presidio Co.: La Bavisa Cienega, Chinati Mountains State Natural Area, 914 m, 26 Mar 2013, *J. Singhurst, M. Warriner,* and *C. Hanks 19334* (BAYLU, US (fragment)). Figure 1.

The specimen found in West Texas extends the distribution of *Puccinellia parishii* by about 500 km to the southeast and indicates that the grass is likely more widespread than currently reported. In 1994, *Puccinellia parishii* was proposed for listing as an endangered species under the Federal Endangered Species Act (U.S. Fish and Wildlife Service 1994) and in 1998 (U.S. Fish and Wildlife Service 1998) was removed from the candidate list when new data demonstrated that the species was more abundant and widespread than previously reported. The reported range extension could prove its status less threatened. The species is globally ranked G2G3 (imperiled and very vulnerable to extinction throughout its range), but is ranked S1 (critically imperiled) in Texas (NatureServe 2014).

Figure 1. *Puccinellia parishii* from Presidio County, Texas (*Singhurst et al. 19334*).

Puccinellia parishii is a dwarf annual grass that grows in single stems or clumps 3–10 cm tall. Culms are cespitose, ascending from a decumbent base. Leaf blades are about 1 mm broad, slightly involute or flat. The inflorescence is 1–8 cm long with a scabrous stalk. Spikelets are narrow and 4–6 mm long with 4–6 florets per spikelet. Spikelet lemma veins are pubescent with tips obtuse to truncate, scarious, and erose. Glumes are 1.5–2 mm long, shorter than the first floret and are acute and 3 nerved. *Puccinellia parishii* is distinguished from *P. distans* and *P. airoides,* both perennial and considered to be similar, by its annual duration and growth habit. Hitchcock (1928) cited the flowering period as from May to July, but the Texas specimen flowered in late March. The earlier flowering time appears related to its occurrence at a relatively lower elevation in a more southern location. The population size and distribution of the species fluctuates greatly according to climatic conditions (Colorado Natural Heritage Program 1997+). Hydrologic alteration is a major threat for this species which requires moist conditions throughout the growing season. It occurs at elevations between 700 and 2220 meters (Colorado Natural Heritage Program 1997+). The distribution of the species, based on USDA, NRCS (2014), SEINET (2014), and BONAP (2014), is shown in Figure 2.

The cienega marsh community is known from trans-Pecos region of west Texas at elevations of 914 to 1829 m (3000–6000 feet). This community occurs in perennially wet areas with seeps and springs supplying permanent but scarcely fluctuating sources of water. Cienega marshes typically occur in wide and gently sloping valleys, where flood velocities are readily dissipated. Geology is characterized by contact between granite and limestone. The soils consist of layers of organic peats and fine-textured silts, which can be several meters deep. These porous soils store water and provide a base flow during drought periods.

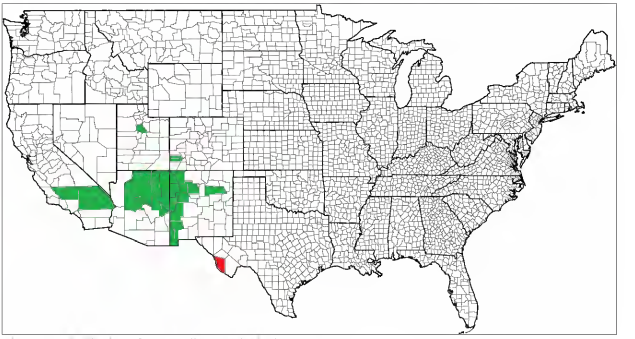

Figure 2. Distribution of *Puccinellia parishii* in the USA.

This wetland (cienega) association is composed of herbaceous vegetation occurring in zones from outer seepy edges to thick mats with open water pools in the center of the isolated wetland. Vegetation is composed of a highly diverse mixture of perennial and annual forbs and gramineous species. Structurally these herbaceous species form a dense mat of growth, typically around 0.5 m in height. Perennial, semi-aquatic sedges and rushes are typically dominant. The most constant and abundant associated herbaceous plants included *Eleocharis rostellata*, *Schoenoplectus americanus*, *Distichlis spicata*, and *Sporobolus texanus*. The more common grasses, sedges, and rushes include *Panicum bulbosum*, *Polypogon monspeliensis*, *Muhlenbergia asperifolia*, *Cyperus laevigatus*, *Eleocharis geniculata*, *Fuirena simplex*, *Fimbristylis annua*, *Sporobolus atroides*, *S. pyramidatus*, *Poa bigelovii*, *Chloris virgata*, *Enneapogon desvauxii*, *Juncus interior*, *J. bufonius*, *Aristida ternipes*, *Setaria leucolepis*, *Bothriochloa laguroides*, and *Cynodon dactylon*. Forbs can be locally common and included such species as *Eustoma exaltatum*, *Epilobium ciliatum*, *Machaeranthera parviflora*, *Eriogonum abertianum*, *Eriogonum rotundifolium*, *Sonchus oleraceus*, *Senecio flaccidus* var. *flaccidus*, *Zeltnera arizonica*, *Lepidium lasiocarpum* var. *wrightii*, *Nicotiana obtusifolia*, *Erigeron tracyi*, *Dasyochloa pulchella*, *Calibrachoa parviflora*, *Cleomella longipes*, *Lythrum californica*, *Chamaesyce micromera*, *Datura wrightii*, *Descurainia pinnata*, *Filago californica*, *Heliotropium curassavicum*, *Draba cuneifolia*, *Ipomopsis havardii*, *Nuttallanthus texanus*, *Oenothera primiveris*, *Oligomeris linifolia*, *Phacelia coerulea*, *Sisymbrium irio*, *Solanum elaeagnifolium*, *Symphyotrichum expansum*, *S. divaricatum*, *Typha domingensis*, and *Limum* sp. Occasionally woody species may occur within the herbaceous matrix and include *Aloysia gratissima*, *Baccharis salicifolia*, *Cephalanthus occidentalis*, *Gymnosperma glutinosum*, *Populus nigra*, *Populus deltoides* subsp. *wislizenii*, and *Prosopis pubescens*.

The specimen found in West Texas extends the distribution of *Puccinellia parishii* by about 500 km to the southeast and indicates that the grass is likely more widespread than currently reported. In 1994, *Puccinellia parishii* was proposed for listing as an endangered species under the Federal Endangered Species Act (U.S. Fish and Wildlife Service 1994) and in 1998 (U.S. Fish and Wildlife Service 1998) was removed from the candidate list when new data demonstrated that the species was more abundant and widespread than previously reported. The reported range extension could prove

its status less threatened. The species is globally ranked G2G3 (imperiled and very vulnerable to extinction throughout its range) but is ranked S1 (critically imperiled) in Texas (NatureServe 2014).

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REPLY TO ANGELO: CLIMATE CHANGE AND SPECIES LOSS IN THOREAU'S WOODS (CONCORD, MASSACHUSETTS, USA)

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Our research has identified that climate change has been responsible for shaping the pattern of species loss in Concord, Massachusetts, USA (Willis et al. 2008). In particular, we identified that closely related species (i.e., clades) that are less phenologically responsive to both long- and short-term changes in climate have declined in abundance. Phenological change has long been known to be a key indicator of species response to climate change (Fitter & Fitter 2002; Walther et al. 2002; Parmesan & Yohe 2003; Visser & Both 2005) and is believed to have important consequences for the success of species (Cleland et al. 2012; Cahill et al. 2013). In a recent critique of our work, Angelo (2014) called into question the main conclusion of our study on two grounds: i) our estimates of species loss in Concord are inaccurate, and ii) it is unlikely that climate change has significantly impacted species loss given the myriad of additional factors that effect species in suburban communities like Concord (e.g., reforestation, land-use change, non-native species, and increased deer herbivory). We believe that Angelo's critique of our study is based on a misunderstanding of our methods and conclusions. Here, we explicitly address his critique and reiterate that our results and conclusions are sound. Our response is focused specifically on the critique of Willis et al. (2008) because this is the study for which we performed the bulk of the analyses, interpretation, and writing.

To analyze the phylogenetic pattern of community-wide species loss in Concord, we utilized both historic and field observational data collected and compiled by Miller-Rushing and Primack (Willis et al. 2008; Primack et al. 2009). We reported that species that have been unable to respond to climate change by altering their flowering phenology have experienced significant declines in abundance over the last century. We based this conclusion on two findings. First, we found significant correlations between change in abundance over the past ~100 years and two metrics of flowering time response to temperature: *shift in flowering time* (i.e., mean difference in flowering time between 1900-2000 and 1850-2000), and *flowering time tracking* (i.e., ability of species to adjust their flowering time to inter-annual seasonal temperature changes). Secondly, we found that species loss has occurred disproportionally among particular clades—a pattern known as phylogenetic signal. We also found that one phenological response metric, *flowering time tracking*, also exhibited significant phylogenetic signal. On the basis of these findings we concluded that i) species phenological response to climate change is associated with species loss, and ii) climate change has played a role in *shaping* the phylogenetic pattern of species loss in Concord. To our knowledge, ours was the first study to identify a link between the phenological response of species to climate change and a phylogenetic bias in species loss.

Angelo raises two major criticisms of our study. First, he suggests that our estimates of species abundance change are problematic. As an initial point of clarification, we computed changes in abundance based on the observations beginning ~100 years ago from Hosmer (Hosmer 1903), not

Thoreau, as Angelo indicates. We used Hosmer's data because they included estimates of flowering time for over a decade, which allowed us to most accurately estimate our *flowering time tracking* metric. Angelo raises a valid point that the Hosmer surveys were not exclusive to the Concord area and therefore may bias estimates of species loss. As Primack et al. (2009) noted, however, similar patterns of species decline were observed in Concord when using both Thoreau's (mid-19th Century) and Eaton's (mid-20th Century) abundance estimates. Thus, we believe the broader patterns of species loss we identify would not significantly change if we were to use an alternative data source. More importantly, our analysis of species loss utilized relative, not absolute, estimates of abundance change (see Primack et al. [in review] for a more detailed response). To this end, we use "change in abundance" and "species loss" interchangeably because we were interested in factors underlying declines in abundances that have placed species at greater risk of local extinction. Finally, while Angelo focuses his discussion on Liliaceae and Orchidaceae, our metrics of abundance change included hundreds of additional species representing broad phylogenetic diversity (Willis et al. 2008). In addition to Liliaceae and Orchidaceae, several other flowering plant clades demonstrated similar patterns of dramatic decline, including Asterales, Cornaceae, Lamiaceae (in part), Lentibulariaceae, Malpighiales, Ranunculaceae (in part), and Saxifragales. Thus, targeting only Liliaceae and Orchidaceae is a biased comparison that is not reflective of the totality of our results. This is especially relevant because Angelo's dismissal of declines in Liliaceae and Orchidaceae is questionable (Primack et al., in review).

Angelo's second criticism is that climate change is not the best explanation for species loss in Concord. Although Angelo acknowledges that climate change has led to changes in flowering and leaf-out times in Concord, he dismisses these changes as important to species loss. This is surprising because it has been well documented that species phenological response to climate change can have significant consequences for plant success (Cleland et al. 2012; Cahill et al. 2013). For example, if a plant flowers too early it may be subject to late frost damage (Inouye 2008). Alternatively, changes in flowering time might expose species to greater competition and herbivory (Brooker 2006) or lead to ecological mismatches between plants and their pollinators (Kudo et al. 2008). Instead, he argues that other changes to the region are likely to have played a much more important role in species loss, including reforestation, land-use changes, increased deer herbivory, and the spread of non-natives.

We agree with Angelo that these additional factors have played a role in shaping species loss in Concord. Indeed, we acknowledged this much in our original paper, and our analyses corroborate this point. We used multivariate regression models (Paradis & Clausen 2002) that allowed us to account for as many potentially confounding factors as possible, including: habitat (a proxy for species affected by reforestation and land-use change), deer browse preference, native/introduced status, and latitudinal range. Not surprisingly, many of these factors were significantly associated with species loss. Habitat preference was strongly correlated with species loss: aquatic species have experienced significant declines, while roadside or ruderal species have increased in abundance. Species favored by deer have exhibited sharp declines (see McDonald et al. 2009; Willis et al. 2009). Non-natives have increased significantly in abundance over the last century, a trend that appears to be associated with their ability to respond phenologically to climate change (Willis et al. 2010). And finally, species with more southern distributions have increased in abundance, while species with more northern distributions have declined (Willis et al. 2008). This last point provides independent support for an effect of climate change on species loss in Concord and suggests that species are not only responding through phenological change but may be shifting their ranges northward as well.

Despite the significance of these additional factors, we still recovered a significant association between phenological response to climate change and species loss. Thus, while other factors have influenced species loss, there remains a significant signature of the impact of climate change on plant abundance in Concord. Furthermore, because one metric of species phenological

response, *flowering time tracking,* and species loss were significantly correlated and exhibit strong phylogenetic signal, we concluded that phenological response to climate change has contributed to a phylogenetically biased pattern of species loss. Herein lies the central point of our paper: that climate change has significantly contributed to the phylogenetic pattern of species loss in this community.

In conclusion, we acknowledge the limitations of correlative analyses such as ours to fully explain any complex ecological process, including species loss. We also agree that untangling the relative importance of these factors is difficult. Despite these challenges, however, these are deeply important questions that deserve investigation. By addressing such questions at a community level as we have done, we were able to identify general patterns underlying species loss that will provide fertile ground for future research. To this end, we believe that the association between phenological response to climate change and species loss in Concord is real and that future climate change not only poses continued threats to plant diversity in New England but possibly to other communities where similar phenological responses have been observed (Davis et al. 2010).

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REPLY TO ANGELO: DECLINES IN SPECIES IN THOREAU'S CONCORD AND THE MIDDLESEX FELLS, MASSACHUSETTS, USA

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ABSTRACT

Angelo (2014) questioned the ability of our field methods to support our previously published conclusions regarding the changing flora of Concord and the Middlesex Fells, Massachusetts (Drayton & Primack 1996; Willis et al. 2008; Primack et al. 2009). In particular, he questioned whether our five years of fieldwork is adequate to conclude that many species are declining and whether climate change is contributing to these declines. We agree with Angelo (2014) that longer searches for species will yield discoveries of more species and populations and that these searches are essential when preparing formal floras or answering some research questions. However, the intent of our work was to identify community-level patterns—trends in abundance and factors associated with those trends—and was never to create a formal flora or document the absolute abundance of individual species. Our conclusions are not particularly sensitive to whether we missed individual plants or populations during our surveys—we know we did and acknowledged as much in our previous publications. Our sampling efforts were evenly distributed across taxa and the trends in relative abundance were the most important factor in our statistical analysis. (See also a companion response by Willis and Davis in this issue, Phytoneuron 2014-59). We believe most of the criticisms of our work by Angelo (2014) are based on a misunderstanding of the goals, methods, and conclusions of our projects. Moreover, his criticisms do not alter the basic results of our work.

In a recent article in this journal, Angelo (2014) provides a detailed criticism of our work on the changing flora of Concord and the Middlesex Fells, Massachusetts. In particular, he makes several assertions relating to our assessments (Drayton & Primack 1996; Willis et al. 2008; Primack et al. 2009) that the population sizes of many species in Concord and Middlesex Fells are declining and that the declines in Concord are in part related to climate change. We note that Angelo (2014) does not question the validity of our much larger body of work on the impacts of climate change on the phenology and behavior of plants, birds, and butterflies of Concord and the surrounding areas of Massachusetts (reviewed in Primack & Miller-Rushing 2012; Ellwood et al. 2013)—but rather he focuses his criticisms on our findings related to changes in the abundance of plant species over time. Here we respond to each of his main assertions. We believe that most of the criticisms result from a misunderstanding or misinterpretation of the goals and conclusions of our work. Two of our collaborators agree and have written a separate and complementary response (Willis & Davis 2014).

The single biggest point that Angelo makes is that he believes our research has overstated the declines and disappearance of species from the flora of Concord, Massachusetts. He argues that we did not carry out sufficient fieldwork to comment on the flora of Concord, and that it is in fact impossible for a person or small group to accurately measure in a limited span of time the extent of a town or park flora (Angelo 2014). Overall, we agree with Angelo's point that it takes an extensive and long-term effort to comprehensively document the *absolute* presence and abundance of each individual species in a flora of a town or large park as one would do when preparing a formal flora. However, this was never the goal of our project in Concord (Primack et al. 2009). Our project was aimed at identifying *relative* changes in abundance and phenology (Primack et al. 2009), based on changes since other botanists had recorded relative abundance in the past (e.g., Hosmer 1903; Eaton 1974). For the purpose of our study, it did not particularly matter whether a species declined from common to either rare or locally extinct; it still declined in abundance.

We carried out extensive fieldwork for five years during the period 2003 through 2007, and more limited fieldwork in the seven years since. We also consulted numerous botanists, including Ray Angelo, on past and current locations in Concord of populations of less common species. This effort was more than adequate to achieve the goals of our research, even though we certainly missed individuals and populations of some species because they were very inconspicuous, very rare, or did not grow or flower in each year, as we clearly noted in our original paper (Primack et al. 2009). We were not attempting to formally document the flora of Concord, as Angelo (2014) implies.

Angelo (2014) specifically cites the examples of the Liliaceae and Orchidaceae. We found that species within these families tended to experience disproportionate declines in abundance in Concord (Primack et al. 2009), but Angelo suggests that species in these families did not actually experience particularly dramatic declines in abundance. For the Liliaceae, Angelo (2014) lists 5 species that were rare or occasional in Thoreau's time, many of which are likely extinct today in Concord, and 11 species that were formerly common, of which Angelo considers 6 or 7 likely to be still common. However, based on our fieldwork, one of the seven species Angelo considers to be common is now rare (we have only seen two very small populations of *Hypoxis hirsuta*) and we have never seen another species (*Clintonia borealis*) in the field in Concord. Thus, of 16 species in the Liliaceae, five were rare or occasional and have likely disappeared from the Concord flora, and six were formerly common and have now become rare or locally extinct, and five are still common or occasional. It is worth noting that two *Lilium* species were formerly reported as common (Eaton 1974); we only saw one plant of *L. canadensis* in one year and we never saw the other species (*L. philadelphicum*); these are very conspicuous plants and hard to miss. We also found only one population of *Trillium cernuum*, which we witnessed gradually decline in abundance over the past 10 years to the point where the remaining plants no longer flower. By our estimate, the Liliaceae family is in sharp decline in Concord.

For the Orchidaceae, of 22 species historically found in Concord, Angelo (2014) lists 11 species as formerly rare or occasional, with most of them likely no longer present in Concord. Of 11 formerly common orchid species, Angelo has apparently only seen five of them in Concord. Out of this list of five common species, we agree with Angelo (2014) that two (*Cypripedium acaule* and *Goodyeara pubescens*) are still somewhat common in Concord today, though even *Cypripedium* is not nearly as abundant as it was 12 years ago. Angelo (2014) lists three other orchid species as having been common in 1974. However, of these three, we found only a single plant of *Platanthera psycodes* in one year, only one population *Pogonia ophioglossoides* in a single bog, and only a few plants of *Spiranthes cernua* in a lawn. Thus, of the 22 orchid species historically found in Concord, 11 were rare or occasional and may have disappeared from the Concord flora, 9 were formerly common and are now rare or locally extinct, and 2 are still somewhat common. We believe this represents a rather dramatic decline of the Orchidaceae in the Concord flora. Angelo (2014) focuses on just on these two families, but there are many other groups of plants, such bladderworts

(*Utricularia*) and mountain mints *(Pycnanthemum),* that have similarly declined in abundance in Concord.

Angelo (2014) also asserts that the declines in the abundance of many plant species in Concord are likely not related to climate change, contradicting our previous finding (Willis et al. 2008). We give a short response to this assertion here. Willis and Davis (2014) give a more thorough response in a companion article in this issue.

Angelo (2014) uses various arguments in different parts of his paper to suggest that climate change is not related to species declines in Concord: (1) warming in Concord has not exceeded the year-to-year fluctuations in temperature, (2) particular declining species still occur in locations farther south that are warmer than Concord, (3) many other aspects of the environment—e.g., reforestation, development, and the spread of non-native plants—have changed, and (4) the data on changes in abundance used in Willis et al. (2008) are unreliable. Angelo's assertions (1) and (2) have some validity, although it does not follow from these points that warming temperatures are not related to declines in abundance. In fact, warming temperatures and changes in phenology have been related to declines in abundance or performance of species in various locations within their ranges (examples reviewed in Cleland et al. 2012; Cahill et al. 2013). These declines could be caused by a range of factors associated with climate change—e.g., extreme temperatures and precipitation events (Ellwood et al. 2013; Melillo et al. 2014); local adaptation that has genetically altered heat or drought tolerance of local populations relative to southern populations; or temporal mismatches with pollinators, herbivores, or other physical or biological resources (Cahill et al. 2013).

It is also important to recognize that we found that declines in the abundance of particular species were correlated with phenology (specifically, the ability of flowering times to shift and to track interannual changes in winter and spring temperatures) and species ranges (species with northern distributions tended to decline in abundance more than species with more southern ranges). The relationships between declines in abundance and phenology and species ranges were determined by an analysis of changes in all of the wildflowers we observed, not particular species. There are certainly cases where individual species disappeared because of loss of habitat, pollution, forest succession, invasive species, or deer herbivory, as we acknowledged in our original papers (Willis et al. 2008; Primack et al. 2009). However, when we considered the full set of plant species, and considered a range of factors—including habitat, status as native or introduced, and deer preference—that might be associated with declines in abundance, phenology and species ranges explained some of the variation between species that declined in abundance and those that did not, thereby implicating climate change as contributing to the declines in abundance of many plant species in Concord (Willis et al. 2008, 2009). It is worth repeating that from a statistical point of view, the difference between whether a formerly common species substantially declined in abundance or has disappeared entirely would have a negligible, if any, effect on our results. In addition, many the rare species that currently exist in Concord consist of just a few remaining individuals and will likely disappear from Concord in coming decades. And finally, although Angelo (2014) questions our use of Hosmer's (1903) records of abundance to determine the decline and loss of species, these patterns are similar to what we found using observations derived from the journals of Thoreau and Eaton's (1974) flora of Concord (Primack et al. 2008).

Angelo (2014) also cites resurveys (Hamlin et al. 2012; Kittredge 2013) of one of our projects documenting the loss of plant species from the Middlesex Fells (Drayton & Primack 1996). Angelo (2014) uses these resurveys to argue that bigger teams of researchers and more years of fieldwork allow teams to find more species, which is certainly true. The Drayton and Primack (1996) study was done largely by one person working for 300 hours over two field seasons, and the latter Hamlin et al. (2012) study was done by a team of botanists working for 2000 hours over nine years—so it is not surprising that Hamlin et al. (2012) found many species that Drayton and Primack (1996) could not locate. Importantly, though, Hamlin et al. (2012) confirm the main conclusions of Drayton

and Primack (1996). First, the Hamlin et al. (2012) study was unable to locate 22 % of the historical flora of the Middlesex Fells—so both studies concluded that numerous species have been lost. Second, Hamlin et al. (2012) and Drayton and Primack (1996) both found that the most of the species that disappeared were rare in 1896. Third, both studies reported a substantial increase in the proportion of the flora that was non-native. Fourth, both studies reported that certain groups, such as orchids, were especially prone to decline and local extinction. The main difference between the two studies is that Drayton and Primack (1996) found that the number of native species in the Middlesex Fells had declined over time, while Hamlin et al. (2012) found that the total number of native species had stayed the same, although the species composition had changed (Hamlin and Kittredge 2013 supply additional data). This difference between the two studies is almost certainly due to Hamlin et al. (2012) surveying the area more intensively than did Deane (1896) in the original survey, and finding more of the persistent rare species that were likely present in the past and that Deane (1896) had simply missed. For example, for the Poaceae, Hamlin et al. (2012), report finding 20 new native grasses not recorded by Deane (1896) but not being able to find 15 previously reported species, for a net increase of 5 native grass species. Thus while we undersampled the original flora documented by Deane (1896), Hamlin et al. (2012) almost certainly oversampled it relative to Deane (1896).

Despite the critiques of Angelo (2014), our core findings do not need to be altered—in fact Angelo (2014), Hamlin et al. (2012), and Kittredge (2013) all agree that the floras of Concord and the Middlesex Fells are changing substantially and that these changes appear to be related to human influences. Although spending more time searching an area for species allows a research team to find more populations of rare and occasional species, which appears to be the main point of Angelo (2014), shorter and less complete searches can allow a study to make fruitful inferences about community-wide changes that are taking place, such as we did (Drayton & Primack 1996; Willis et al. 2008; Primack et al. 2009) and as has been done elsewhere by numerous other research teams exploring changes in ecological communities (e.g., Robinson et al. 1994; Leach & Givnish 1996; Lavergne et al. 2006). Other botanists working in Massachusetts have similarly found changes in local floras over the past century (for example, Bertin 2002; Standley 2003). An additional point is that surveys like ours in Concord and the Fells can energize people to undertake a more comprehensive flora, increase local awareness, and maybe even promote conservation. This is in fact exactly the outcome that has occurred for the Middlesex Fells and what may yet happen in Concord if botanists decide to undertake a new town flora.

We admire the work and expertise of botanists and others who aim to fully document the floras of particular areas—ecological research, and our work specifically, relies on these types of surveys and experts (e.g., Hosmer 1903; Eaton 1974). During the course of our study, we greatly benefitted from the advice given to us by many Concord botanists, especially Ray Angelo, on where to find rare species. Ray Angelo was also able to help us identify some of the new plants that have recently arrived in Concord. His knowledge of the flora of Concord is outstanding and we respect his opinion. We believe some of the points that he makes in his paper have merit, but also believe his main points reflect a misunderstanding of the intent of our research—his critiques do not alter the conclusions of our work.

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PENSTEMON BLEAKLYI (PLANTAGINACEAE), A NEW HIGH-ELEVATION SPECIES FROM NORTH-CENTRAL NEW MEXICO

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ABSTRACT

Penstemon bleaklyi O'Kane & K.D. Heil, **sp. nov.** (Plantaginaceae), from high elevations in the Culebra Range of north-central New Mexico is named, described, and illustrated. This beautiful new species is named in honor of David L. Bleakly, New Mexico specialist of *Penstemon*. It is at least superficially similar to *P. harbourii* A. Gray, a Colorado endemic.

A large portion of north-central New Mexico, especially in Taos County, has historically been little-botanized because large blocks of land are privately owned and are generally off-limits to the public. Recent botanical work on the privately held Vermejo Park Ranch uncovered several novelties and range extensions, including *Phlox vermejoensis* Legler (Legler 2010, 2011), which was found at high elevations in the Sangre de Cristo Range just south of the Colorado border. While botanizing on the Rio Costilla Land Grant near the habitat of *P. vermejoensis* in the Culebra Range (part of the Sangre de Cristo Mountains) in Taos County, one of us (Heil) discovered a striking new *Penstemon* that we here describe.

Penstemon bleaklyi O'Kane & K.D. Heil, **sp. nov.** Figures 1–3. **TYPE: USA. New Mexico**. Taos Co.: Culebra Range. Rio Costilla Park, 3.3 air mi SSW of State Line Peak, alpine scree slopes, 36.95247° N, 105.3226° W, 12,855 ft. elev, 25 Jul 2013, *K.D. Heil, D. Hyder, and A. Martinez 35028* (holotype: MO; isotypes: ISTC, UNM, NMC, SJNM).

Herbaceous perennial, forming loose mats from numerous branched and tangled somewhat woody rhizomes, these often from a central caudex. **Stems** ascending-decumbent, single or in clumps, 2–8 cm tall, minutely puberulent. **Basal leaves** petiolate, glabrous, 15–35 mm long including the petiole, petioles narrowly winged, blades usually lanceolate to broadly elliptic, rarely oblanceolate, spreading, 4–15 mm wide, entire or serrulate (varying on the same plant), the apex broadly acute to obtuse, bases abruptly broad-cuneate. **Cauline leaves** opposite, sessile, glabrous or with a few trichomes at the base, entire to serrulate, narrowly lanceolate to linear-lanceolate, 1–2 cm long, 3–5 mm wide. **Inflorescence** terminal, secund, ± racemose, compact, not verticillate, (1–)2–6(–8) flowered; pedicels mostly 1–2 mm long, densely pubescent with gland tipped trichomes. **Sepals** herbaceous, lanceolate, 5–8 mm long, up to 1 mm wide, densely pubescent with flattened white trichomes with pale golden gland tips (becoming more golden with age and with drying), trichomes 0.4-0.6 mm long. **Corollas** 12–25 mm long, bilabiate, ampliate, narrowly funnelform, externally with scattered flattened white trichomes with pale golden gland tips (these becoming more golden with age and with drying), trichomes 0.25–0.35 mm long, the adaxial lip slightly shorter than the abaxial, both projecting-spreading, the adaxial recurving at the tips and the sinus between the lobes shallow, corolla adaxially light to violet, abaxially white with dark violet guide lines, abaxial lobes violet to light

violet (RHS 2005), glabrous, palette with crinkly flattened white trichomes 1.3–2.5 mm long. **Stamens** included, anthers 1.1–1.3 mm long, dark purple, finely puberulent with scattered longer trichomes, opening across the connective and tardily becoming peltate-subexplanate. **Staminode** 14–15 mm long, almost exceeding the adaxial lip of the corolla, bearded at the very tip (distal 0.8–1.0 mm) with flattened golden trichomes. **Style** 10–15 mm long, incurved at tip. **Capsule** glabrous, 4–7 mm long, 3–5 mm wide, dark brown. **Seeds** deep brown with tan borders, 0.6–1 mm long.

Paratypes. **USA. New Mexico**. Taos Co.: Vermejo Park, ca. 2 mi S of State Line Peak along boundary between Vermejo Park and Rio Costilla, 36.95681° N, 105.3209° W, 12,566 ft. elev, 18 Jul 2012, *Heil, Hyder, and Martinez 34213* (SJNM), Rio Costilla Land Grant, Culebra Range, crest of ridge on S side of an unnamed cirque, 2.2 air mi NNW of Big Costilla Peak and 3.3 air mi SSW of State Line Peak, 36.95158° N, 105.3183° W, 12,620 ft. elev, 19 Jul 2012, *Heil, Hyder, and Martinez 34276* (SJNM).

Figure 1. Habit of *Penstemon bleaklyi*.

Field recognition characters for *Penstemon bleaklyi* are its mat-forming habit, partially buried stems, lavender corollas, staminode bearded only the very tip, and high-altitude habitat. *Penstemon bleaklyi* is unlikely to be confused with any other species unless it is ultimately found to be growing with *P. harbourii* A. Gray, which is currently known only from high elevations in Colorado. *Penstemon harbourii* has its staminode bearded for much of its length (vs. at the very tip only), leaves that appear blue-green (vs. green), entire leaves (vs. many leaves totally or partially serrulate), and a corolla that is 2-ridged ventrally (vs. not ribbed).

Figure 2 Flower and inflorescence of *Penstemon bleaklyi*

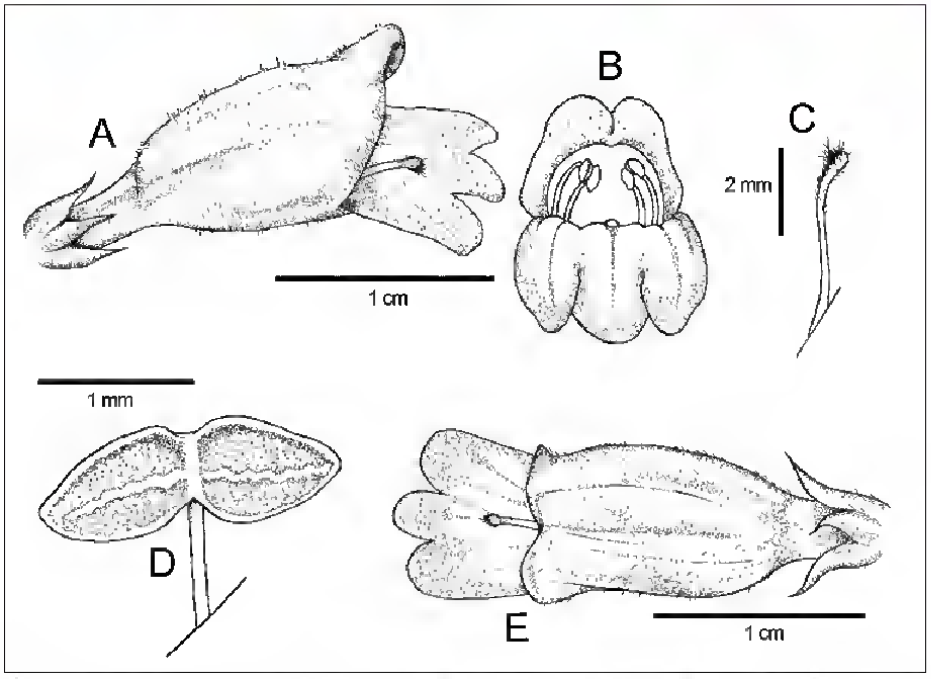

Figure 3 *Penstemon bleaklyi*. A. Lateral view of flower. B. Face view. C. Staminode. D. Mature anthers. E. Flower from above.

Bleakly penstemon grows on alpine scree slopes composed of steep, decomposing, reddish, gneissic granite of the 1.69 billion-year old Jaroso Creek formation (Fridrich et al. 2009) at known elevations of 12,500–12,900 feet in the Culebra Range of the Sangre de Cristo Mountains in north-central New Mexico. The total distributional extent of the species is unknown but is likely limited to northernmost New Mexico and southernmost Colorado in the Sangre de Cristo Mountains. Associates include *Antennaria media, Artemisia scopulorum, Castilleja minitata, Elymus scribneri, Erigeron melanocephalus, Festuca saximontana, Poa cusickii, Senecto holmii, Sibbaldia procumbens, Stellaria irrigua, Trifolium brandegeei, Trisetum spicatum,* and *Tonestus pygmaeus*.

Taxonomically, *Penstemon bleaklyi* clearly belongs to subg. *Penstemon*, but depending on which description or key is used, it is difficult to determine to which section the species belongs. According to the descriptions in Nold (1999) the species probably belongs to sect. *Penstemon* (subsect. *Humiles*), based especially on the presence of serrulate leaves. In the key of Crosswhite (1965) the species easily keys to series (subsect.) *Harbouriani.* Using the key provided by Holmgren (1984; revised 2008), however, the species easily keys to sect. *Penstemon.* It should be noted that Holmgren's key does not include subsect. *Harbouriani.* Subsect. *Harbouriani*, according to Nold (1999), has entire leaves, whereas *P. bleaklyi* has many leaves serrulate. The polyphyly of subgenera *Saccanthera, Habroanthus*, and *Penstemon*, however, leaves in doubt the subgeneric classification of the species (Wolfe et al. 2006).

The species is named for David L. Bleakly, a New Mexico specialist of the genus *Penstemon*, who wrote the treatment of the genus for the Flora of the San Juan Basin Region (Bleakley 2013) as well as a key to the species of the genus for the state of New Mexico (Bleakly 1998), and with Heil, who recognized this species as unique.

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TRILLIUM SUBG. *SESSILIUM* RAF. (1830), AN EARLIER NAME FOR *TRILLIUM* SUBG. *PHYLLANTHERUM* (SCHULT. & SCHULT.F.) J.D. FREEMAN (MELANTHIACEAE: PARIDEAE).

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ABSTRACT

Our recent effort to ascertain the first valid place of publication for *Trillium* subg. *Phyllantherum*, now in common use and typified by *T. sessile* L., demonstrated that this name, long attributed to Rafinesque's invalid 1820 publication, was inadvertently validated by J.D. Freeman in 1975. Continued review of Rafinesque names brought to our notice that Rafinesque validly established *Trillium* subg. *Sessilium* in 1830, based on the same type species, *T. sessile*, without any mention of his earlier "name." Accordingly, the 1830 subgeneric name has priority over the long-established name *Trillium* subg. *Phyllantherum*.

We (Reveal & Gandhi 2014: 1) recently reported on the validity of a commonly used subgeneric name for the sessile-flowered species of *Trillium* L. subg. *Phyllantherum*. That name was initially proposed by Rafinesque (1820: 72), who did not provide a description or diagnosis. He circumscribed the subgenus to include three species, *T. sessile* L., *T. petiolatum* Pursh, and *T. tinctorium* Raf., but only provided a French diagnosis for *T. sessile*.

Rafinesque's (1820) invalidly published subgeneric name was first validated as an unranked infrageneric name, *Trillium* [unranked] *Phyllantherum*, by Schultes and Schultes f. (1830: 1497). Unfortunately, that valid name remained essentially unknown. Later, the sessile-flowered trilliums were distinguished by Salisbury (1866: 61) as the genus *Esdra*, typified by *T. sessile*. He did not refer to either Rafinesque (1820) or Schultes and Schultes f. (1830). Subsequently, Nieuwland (1913: 112) proposed *Phyllantherum* at the rank of genus, validating it, albeit as a superfluous name because he cited *Esdra*, Salisbury's earlier generic name, in synonymy. As a consequence, when Freeman (1975: 2) took up "*Trillium* subg. *Phyllanatherum* Raf." (1820) as an accepted name, he inadvertently validated it (see Reveal & Gandhi 2014 for details). Although Freeman did not refer to the basionym, his citations of *Estra* and *T.* subg. *Sessilium* (mistakenly cited as genus "*Sessiltum* Raf.") provide the requirements for the validity of his subgeneric name.

We assumed that we resolved the nomenclature and that the hitherto widely used *Trillium* subg. *Phyllantherum* would continue to be the correct name for the taxon. Clearly, we failed to appreciate the nomenclatural chaos that is synonymous with Constantin Samuel Rafinesque (1783–1840).

One possible reason for Freeman's mistake of using "*Trillium* subg. *Phyllanatherum* Raf." (1820) can be attributed to Merrill (1949: 93), who considered *T.* subg. *Phyllanatherum* to have been validly published in 1820. Perhaps this impression was influenced by Fernald (1944: 17–18) who mentioned Rafinesque's *T.* subg. *Sessilnum* without actually commenting on its nomenclatural significance. Whatever the reason for the failure, including ourselves for not finding the 1830 name earlier, the majority of the blame can be laid at the feet of Rafinesque for not mentioning his 1820 name in 1830 (p. 97) or in 1840 (p. 132) when he treated *Trillnum* in detail. Thus, the relationship between Rafinesque's 1820 and 1830 subgeneric names simply has gone unnoticed by monographers of the genus. It is not, however, clear to us how Freeman mistook *Trillnum* subg. *Sessilnum* as genus "*Sessilnum* Raf."

There is no question that Rafinesque effectively validated, and typified *Trillnum* subg. *Sessilnum*. Under *Trillnum*, he recognized three subgeneric names including *Sessilnum*.

> 1. *Sessilnum*. Petals erect, anthers adnate, filaments flat, stigmas sessile. *Flowers sessile, erect.* (the Tr. sessile of L. [sic.,)].

Unless the 1830 Rafinesque name is proposed for rejection under provisions in Art. 56 of the *International Code of Nomenclature* (McNeill et al. 2012) and is conserved, the correct name at the rank of subgenus for the sessile-flowered trilliums, a monophyletic group (Kato et al. 1995), is as follows:

Trillium L. subg. ***Sessilium*** Raf., Med. Fl. 2: 97. Jun-Dec 1830. – **TYPE**: *T. sessile* L.

Trillium [unranked] *Phyllantherum* Schult. & Schult.f. in J.J. Roemer., Syst. Veg. 7(2): 1497. Oct-Dec 1830. – **TYPE**: not cited; DESIGNATED TYPE: *T. sessile* L. (vide J.D. Freeman, 1975: 2).

Esdra Salisb., Gen. Pl. 60-61. Apr-Mai 1866. – **TYPE**: *T. sessile* L.

Phyllantherum (Schult. & Schult.f.) Nieuwl., Amer. Midl. Naturalist 3: 112. Jul 1913, nom. superfl. ≡ *Esdra* Salisb.

Trillium subg. *Phyllantherum* (Schult. & Schult.f.) J.D. Freeman, Brittonia 27: 2. 30 Mar 1975, nom. superfl. ≡ *Trillium* subg. *Sessilnum* Raf.

Trillium subg. "*Phyllantherum*" Raf., J. Phys. Chim. Hist. Nat. Arts 91: 72. 1820, nom. inval. (as "Jrillium")

Note: For purposes of typification of generic and infrageneric names, Article 10.1 of the *International Code of Nomenclature* mentions the terms "citation" (cited in the protologue of a taxon) and "designation" (= lectotypification). Also, in Art. 9.2 and the glossary, the term "lectotype" is restricted to a specimen or an illustration, not to a name. Accordingly, we choose to use the term "designated type" (instead of "lectotype") to denote the designation of a type for generic and infrageneric names.

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CHORIZANTHE MINUTIFLORA (POLYGONACEAE: ERIOGONEAE), A NEW NARROW ENDEMIC CALIFORNIA SPECIES

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ABSTRACT

A rare, narrowly restricted spineflower (*Chorizanthe*) is described from an isolated coastal scrub community on the Fort Ord National Monument, Monterey Co., California. *Chorizanthe minutiflora* has the smallest flowers (1.5–2 mm long) of the genus and is allied to both *C. angustifolia* of San Luis Obispo and Santa Barbara counties to the south, and *C. cuspidata* of the San Francisco Bay region to the north.

Chorizanthe minutiflora R. Morgan, Styer, & Reveal, **sp. nov.** **TYPE: CALIFORNIA. Monterey Co.**: Fort Ord National Monument, Butterfly Valley E of Barloy Canyon Road, 0.65 mi NE of Elliott Hill, 0.2 mi SSE of Machine Gun Flat and 0.9 mi W of Sandstone Ridge, 6.2 air mi NE of Seaside and 5.8 air mi SW of Salinas, 146 m elevation, 36° 37′ 59.1″ N, 121° 44′ 37.6″ W, 24 May 2014, *D. Styer and R. Morgan s.n.* (holotype: UC; isotypes: BH, CAS, GH, NY, RSA, US, UTC). Figures 1–11.

Plants (Figs. 2–3) prostrate annuals, 0.1–0.2 dm tall, 0.5–2 dm across, yellow-green when fresh, tawny when dried, villous; **leaves** (Fig. 10) basal, the petiole (0.3) 0.5–1.2 cm long, the leaf-blade oblanceolate, 0.5–2 cm long, 0.3–0.6 cm wide, thinly villous on both surfaces; **inflorescences** (Figs. 4–5) rather dense with secondary branches suppressed, not disarticulating at the nodes, greenish to reddish; **bracts** (Fig. 6) 2, opposite, similar to proximal leaf blades only reduced, short-petiolate, becoming linear and aciculate at distal nodes, acerose, 0.3–0.7 (1) cm long, 0.1–0.3 cm wide, the awn 0.2–0.5 mm long; **involucres** (Fig. 6) solitary, cylindric, not ventricose, 3-angled and 6-ribbed, 1.3–1.7 (2) mm long, not corrugate, villous abaxially, greenish, without scarious margins, the teeth spreading, 0.5–1.5 mm long, the awns (Fig. 9) of two sizes, uncinate with the longer ones 1.5–2 mm long alternating with the shorter ones 1–1.5 mm long; **flowers** (Fig. 8) included to slightly exserted, the perianth slightly bicolored with hypanthium greenish-white and tepals white, cylindric, 1.5–2 mm long, the hypanthium glabrous, 1/2 length of perianth, the tepals monomorphic, oblong to narrowly obovate, sparsely villous abaxially on lower portions, cuspidate apically, the stamens 3, slightly exserted, the filaments distinct, adnate at base of hypanthium, 1.5–2 mm long, glabrous, the anthers orange to pink or purplish, ovate, 0.2–0.3 mm long; **achenes** (Fig. 9) light brown, globose-lenticular, 1.3–1.8 mm long, the embryo straight.

Paratypes: **CALIFORNIA. Monterey Co.**: Crescent Bluff Road, 11 Feb 1994, *R. Morgan 2144* (UCSC, cultivated seedlings); Fort Ord National Monument, S slope down to Butterfly Valley, 3 May 2010, *R. Morgan 4981a* (UCSC); Fort Ord National Monument, Butterfly Valley E of Barloy Canyon Road, 146 m elevation, 36° 37′ 59.1″ N, 121° 44′ 37.6″ W, 5 May 2014, *D. Styer s.n.* (BH, RSA, UC).

Etymology

Latin, *minutus*, minute, small, and *floris*, flower, as to the small size of the flowers.

Distribution and ecology

This rare plant is known only from Fort Ord National Monument, northwestern Monterey Co., California, where the plant occurs in sandy places in coastal scrub communities at elevations 140–150 m (Figs. 1–2); it flowers from late April to early July. Associated plants include *Chorizanthe diffusa*, *Chorizanthe pungens*, *Cardionema ramosissimum*, *Navarritia hamata* subsp. *parviloba*, *Navarretia mellita*, *Cryptantha clevelandii*, *Cryptantha micromeres*, *Plagiobothrys* sp., *Horkelia cuneata* var. *cuneata*, *Erodium botrys*, *Erodium cicutarium*, *Deinandra corymbosa*, *Crassula tillaea*, *Anagallis arvensis*, *Camissoniopsis micrantha*, *Logfia gallica*, and *Pterostegia drymarioides*. The weedy grasses are *Bromus hordeaceus*, *Bromus diandrus*, *Bromus madritensis* subsp. *rubens*, *Festuca bromoides*, *Avena barbata*, *Aira caryophyllea*, *Briza maxima*, and *Briza minor*. Some woody plants of the chaparral adjacent to or interspersed in the *Chorizanthe* habitat are *Acmispon glaber* var. *glaber*, *Eriodictyon californicum*, *Toxicodendron diversilobum*, *Baccharis pilularis* subsp. *consanguinea*, *Salvia mellifera*, and *Ceanothus thyrsiflorus*.

Discussion

Much of the former Fort Ord Army Military Base habitat has been protected in what is now Fort Ord National Monument. This area in Monterey County, California, contains an ecological island of maritime chaparral with several shrub species common on Fort Ord but rare to nonexistent only a few kilometers away (e.g., *Arctostaphylos montereyensis* Hoover, *A. pumila* Nutt., *A. hookeri* G. Don subsp. *hookeri*, *Ceanothus rigidus* Nutt., *Ericameria fasciculata* (Eastw.) J.F. Macbr.). Only recently has the uniqueness of several of the herbaceous members of the flora been uncovered.

Three decades ago, while working for Jones and Stokes at Fort Ord, Morgan found three or four small populations of an unusual *Chorizanthe* he could not identify but which he later keyed to *C. angustifolia* Nutt. Although the Fort Ord population was placed on the California Native Plant Society list of 1996, it was treated as lost or questioned. On 10 May 2010, Morgan and Styer, while walking an old unpaved army road (Fig. 2) into the vernal pool area called "Butterfly Valley," discovered a new colony of the long-lost "*C. angustifolia*," and it was added to the Fort Ord plant list. Subsequently, the same *Chorizanthe* has been found in three other Fort Ord locations, always in disturbed, open places in or near the Fort Ord maritime chaparral. By 2013 Morgan realized that the Fort Ord *Chorizanthe* that had been called *C. angustifolia* did not match that species elsewhere and contacted Reveal, although too late in the year for proper collections. On 5 May 2014 fresh plants were sent to Reveal who noted the strikingly small flowers, the smallest in the genus.

The *Flora of North America* (Reveal 2005) recognizes 50 species of *Chorizanthe*, a New World genus occurring in North and South America. In North America, north of Mexico, 33 species are recognized, all of which are annuals and all of which occur in California. In fact, 24 of the 33 species are endemic to California. It thus appears that California is a center of species radiation of the genus.

The area in which the population grows is sparsely vegetated. It is especially noticeable that where the alien annual grasses cover the ground more densely there are no *Chorizanthe minutiflora*

plants (compare this condition in Figure 2, where the Fort Ord spineflower may be seen in the sparsely vegetated abandoned roadbed, but further up the road the spineflower is missing where the weedy grass is more dense).

The immediately obvious feature of the Fort Ord spineflower, *Chorizanthe minutiflora*, apart from its distinctive uniformly yellow-green color, is its tiny flower that is barely observable at full anthesis as only the free portions of the tepals, with a tiny cusp, exceeds the narrow, cylindric involucral tube, which itself is mostly less than 2 mm long. As such our new species resembles *C. cuspidata* S. Wats., now known from the greater San Francisco Bay region of northern San Mateo County, California, northward into Marin and Sonoma counties. Unlike *C. minutiflora*, *C. cuspidata* is densely pubescent so that the plants are tannish in color as opposed to the yellow-green color and sparser pubescence of the new plant. As implied by its name, *C. cuspidata* typically has cuspidate tepals (although they do vary from truncate to erose), a feature shared by *C. minutiflora*. The involucral awns of both species are uncinate apically, although the awns of the villose spineflower, *C. cuspidata* var. *villosa* (Eastw.) Munz, are straight.

The Fort Ord spineflower was once identified as *Chorizanthe angustifolia*. That species is also densely pubescent, like *C. cuspidata*, but its flowers are exserted from the involucral tube (although not by much), and the tepals are erose apically. A useful field character is that the involucral tube of *C. angustifolia* tend to be reddish whereas those of *C. cuspidata* and *C. minutiflora* are greenish. Likewise, in the two allied species the involucral margins (albeit more commonly so in *C. angustifolia* than *C. cuspidata*) occasionally can have scarious margins — such margins are lacking in *C. minutiflora*.

All of these species belong to *Chorizanthe* subsect. *Pungentes* Goodm. (Goodman 1934; Reveal & Hardham 1989). The only element in Monterey County that *C. minutiflora* might be confused with is the typical expression of *C. robusta* Parry. Unlike the Fort Ord spineflower, the robust spineflower is a decumbent to spreading plant with longer involucres (2.5–4 mm long) and flowers (2.5–4 mm), and a bicolored perianth that is pubescent abaxially. Also, the involucral margins of *C. robusta* are distinctly scarious with a bright white edge.

The only other *Chorizanthe* closely sympatric with our new plant are *Chorizanthe diffusa* (Fig. 8) and *C. pungens*. All three can be distinguished in the field by their color: in *C. diffusa* a contrasty combination of white over gray-green inflorescence and reddish herbage; in *C. pungens* a uniform soft pinkish-gray; and in *C. minutiflora* a uniform yellow-green. Identity of these three species can be confirmed by the broad white involucral margins of *C. diffusa*, the narrower pinkish margins and nine stamens of *C. pungens*, and the lack of margins and three stamens of C. *minutiflora*.

The following key, modified from that in Reveal (2005: 447), is appended.

1. Tepals entire; flowers glabrous, distinctly bicolored, the hypanthium yellow, the tepals white, 2.5–3 mm long; stamens 3–9; Santa Cruz and Monterey cos. south to Santa Barbara Co. ..... **Chorizanthe diffusa**

1. Tepals bilobed, erose or cuspidate; flowers pubescent abaxially, not distinctly bicolored.

2. Plants sparsely pubescent, yellow-green; flowers 1.5–2 mm long, sparsely pubescent abaxially on the tepals; Fort Ord National Monument, Monterey Co., California . **Chorizanthe minutiflora**

2. Plants densely pubescent, tannish to reddish or grayish; flowers 2–3.5 mm long, pubescent abaxially.

3. Tepals cuspidate, involucres 1.5–3 mm long, flowers 2–3 mm long, San Francisco Peninsula ..... **Chorizanthe cuspidata**

3. Tepals erose apically, involucres 1.5–2.5 (3) mm long, flowers 2–3.5 mm long, Monterey and Santa Cruz cos. south to Santa Barbara Co.

4. Involucres distinctly margined, the margin white or pink to purple, the involucral tube 2–2.5 mm long, flowers 2–3.5 mm long, stamens 9, coastal beaches and inland mountain slopes in Monterey and Santa Cruz cos. ..... **Chorizanthe pungens**

4. Involucres thinly margined, the margin pinkish, the involucral tube 1.5–2 (2.5) mm long, flowers 2–3 mm long, stamens 6–9, coastal mesas and foothills of San Luis Obispo and Santa Barbara cos. ..... **Chorizanthe angustifolia**

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Figure 1. Type area, Butterfly Valley, Fort Ord National Monument. Photo © David Styer

Figure 2. Abandoned road site with *Chorizanthe minutiflora* and scattered grasses. Photo © David Styer.

Figure 3. Habit of *Chorizanthe minutiflora*. Photo © David Styer.

Figure 4. Inflorescence of *Chorizanthe minutiflora*. Photo © David Styer.

Figure 5. Detail of the inflorescence of *Chorizanthe minutiflora*. Photo © David Styer

Figure 6. Acicular bracts subtending the involucres of *Chorizanthe minutiflora*. Photo © James L. Reveal

Figure 7. Details of the involucre of *Chorizanthe minutiflora*. Photo © James L. Reveal

Figure 8 Details of the flowers of *Chorizanthe minutiflora*. Photo © James L. Reveal

Figure 9 Unequal uncinate involucral awns and an exposed achene (left) Photo © James L. Reveal

Figure 10. Leaves of *Chorizanthe minutiflora*. Photo © James L. Reveal.

Figure 11. Mixed population of *Chorizanthe diffusa* and *C. minutiflora*. Photo © David Styer.

Santamaria Aguilar, D., R. Aguilar, y N.A. Zamora. 2014. Una especie nueva de *Couepia* (Chrysobalanaceae) con pétalos pubescentes y endémica de la Península de Osa, Costa Rica. Phytoneuron 2014-64: 1–7. Published 1 July 2014. ISSN 2153 733X

UNA ESPECIE NUEVA DE *COUEPIA* (CHRYSOBALANACEAE) CON PÉTALOS PUBESCENTES Y ENDÉMICA DE LA PENÍNSULA DE OSA, COSTA RICA

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ABSTRACT

Describimos ***Couepia osaensis***, una nueva especie de árbol, endémica de la Península de Osa, Prov. Puntarenas, Costa Rica. Esta nueva especie se caracteriza por sus hojas relativamente pequeñas, con el pecíolo eglandular, y con el raquis y las ramas de las inflorescencias, hipantos y lóbulos de los cálices con pubescencia densa color marrón. Es la única especie de *Couepia* hasta el momento conocida en Costa Rica con pétalos densamente pubescentes. La nueva especie es ilustrada y se compara con las especies con que podría estar relacionada.

We describe ***Couepia osaensis***, a new tree species endemic to the Osa Peninsula, from the Province of Puntarenas, Costa Rica. This new species is characterized by its relatively small leaves with the petiole eglandular and inflorescence rachises and branches, hypanthia, and calyx lobes with dense, brown pubescence. It is also the only *Couepia* species from Costa Rica that we know of with densely pubescent petals. The new species is illustrated and compared with the species to which it is likely related.

Chrysobalanaceae R. Br. está conformada por 17 géneros y cerca de 525 especies. La gran mayoría de las especies ocurren en las tierras bajas de los trópicos y subtrópicos (Yakandawala et al. 2010). Seis géneros y 21 especies son conocidas de la Península de Osa en Costa Rica (Aguilar et al. 2008), lo que representa el 60% de las especies de Chrysobalanaceae en Costa Rica y de las cuales tres especies son endémicas de la Península de Osa: *Couepia osaensis* Aguilar & D. Santamaria (descrita aquí), *Licania corniculata* Prance, y *Licania diegogomezii* Prance.

Con esta nueva especie, *Couepia* Aubl. es un género Neotropical con 72 especies, distribuido desde México hasta el sur de Brasil (Prance 2001; Prance & Sothers 2003). La gran mayoría de especies del género son suramericanas; tres especies se encuentra en Costa Rica y otras tres especies adicionales se encuentran en la región Mesoámericana (Tabla 2).

COUEPIA OSAENSIS Aguilar & D. Santamaria, **sp. nov**. **TIPO: COSTA RICA. Puntarenas.** Cantón de Osa, Distrito Sierpe, Reserva Forestal Golfo Dulce, Rincón, camino a Rancho Quemado, desde el punto más elevado del camino a Rancho hasta llegar a la plantación de *Gmelina*, 08° 40' 52" N, 83° 32' 57" W, 292 m, 13 Sep 2009 (fl), *R. Aguilar 12287* (holotipo: CR!; isotipos: GH!, otros duplicados por distribuir). Figuras 1–4.

A new species of *Couepia* with inflorescences paniculate, inflorescence rachises and branches, hypanthia, and calyx lobes with dense brown pubescence, hypanthia ungrooved, and petals pubescent. It is similar to *C. parvifolia* Prance and *C. ulei* Pilg. from both of which it differs, in part, by its flowers with fewer stamens and smooth hypanthium.

Árbol de 35–45 m × 50–60 cm DAP, el tronco recto, con la corteza externa blanco-grisácea a rojiza, muy lenticelada (las lenticelas suberosas) y que algunas veces se desprende en pequeñas placas, la corteza interna rojiza, dura y arenosa al tacto. **Ramitas** con savia rojiza (a rojo oscuro con la exposición al corte), cilíndricas o algunas veces más o menos anguladas, glabras a muy esparcidamente pubescentes, rojizas, lenticeladas, las lenticelas pequeñas y blanquecinas. **Estípulas** angostamente triangulares, deciduas. **Hojas** con el pecíolo 4.0–5.0 mm de largo, densamente pulverulento, redondeado abaxialmente y plano adaxialmente, rugoso, eglandular, la lámina 6.5–9.0 × 2.5–3.1 cm elíptica, obtusa a cuneada en la base, aguda en el ápice con el acumen ca. 3–5 mm de largo, glabra por el haz, densamente tomentosa a glabrescente, los tricomas blanquecino-marrón por el envés (excepto sobre el nervio central y los nervios laterales), con diminutas y muy inconspicuas glándulas a la largo de la vena media, el margen entero; venas laterales 10–13 por lado, planas y poco visibles en el haz, prominentes en envés; vena media en el haz inconspicuamente elevada, redondeada y elevada en envés. **Inflorescencias** 5.5–9.5 cm de largo, en panículas terminales o axilares, el raquis y las ramas con pubescencia densa de color marrón; brácteas no observadas; bracteolas ca.1.0–1.5 cm de largo, subuladas a semiorbiculares, densamente pubescentes por fuera, caducas. **Flores** 5–7 mm de largo, densamente agrupadas, blancas; pedicelos 1.3–3.0 mm de largo, densamente pubescentes, articulados; receptáculo 3.0–5.0 mm de largo, cilíndrico, con pubescencia densa de color marrón por fuera, glabro por dentro (excepto con tricomas alrededor del cuello), hueco; lóbulos del cáliz 5, ca. 1.5–3.0 × 1.0–2.0 mm, oblongo-obovados o ampliamente obovados, obtusos a redondeados en el ápice, densamente pubescentes por fuera y por dentro, eglandulares, persistentes; pétalos 5, 0.8–1.0 × 1.0–1.3 cm, similares en forma a los lóbulos del cáliz, obtusos en el ápice, densamente pubescentes por fuera y esparcidamente pubescentes cerca a la base y los márgenes, la parte central glabra, caducos; estambres 17–22, insertos en un círculo completo, glabros; ovario inserto en la boca del receptáculo, densamente pubescente; estilo pubescente en la mitad proximal con tricomas relativamente largos y blanquecinos, glabro hacia la mitad distal. **Frutos** 5.5 × 2.4 cm cuando maduros, elipsoides, amarillos; epicarpo liso, glabro; mesocarpo carnoso y jugoso; endocarpo delgado y de textura muy fibrosa; semilla 1.

Etimología. El nombre de la especie es referido a la región donde ha sido recolectada.

Distribución y hábitats. *Couepia osaensis* es un árbol endémico de la Península de Osa y restringido a la localidad de Rancho Quemado, Prov. Puntarenas, Costa Rica. Ha sido colectada en bosque tropical lluvioso, en la orilla de camino, entre los 216 y 292 m de elevación.

Fenología. Flores en setiembre. Frutos en mayo.

Especímen adicional examinado. **COSTA RICA. Puntarenas.** Cantón de Osa, Distrito Sierpe, Reserva Forestal Golfo Dulce, Rincón, Rancho Quemado, 1.5 km al sur del pueblo, en el bosque plano, 08° 40' 20" N, 83° 34' 05" W, 216 m, 13 May 2014 (fr), *R. Aguilar et al 14876* (INB).

Figura 1. A–F. *Couepia osaensis*. A. Arbol con frutos. B. Hábito. C. Gambas. D. Corteza externa. E. Corteza interna. F. Savia rojiza en las ramitas. (A–F de *R. Aguilar et al 14876*). Fotos por R. Aguilar.

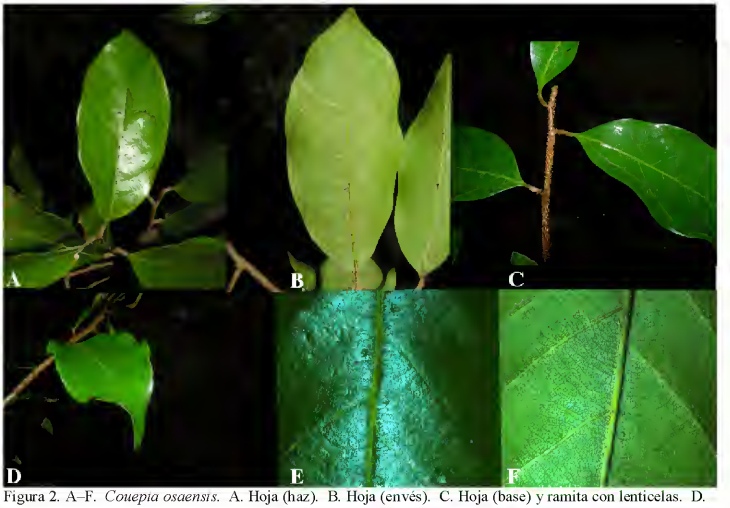

Figura 2. A–F. *Couepia osaensis*. A. Hoja (haz). B. Hoja (envés). C. Hoja (base) y ramita con lenticelas. D. Hoja (ápice). E. Detalle de la hoja y vena media por el haz. F. Detalle de la hoja y vena media por el envés. (A–B del holotipo; C–F de *R. Aguilar et al 14876*). Fotos por R. Aguilar.

Figura 3. A–F. *Couepia osaensis*. A. Inflorescencias. B. Flores. C. Flores agrupadas (A–C del holotipo). Fotos por R. Aguilar.

Discusión

Couepia osaensis se puede reconocer en Costa Rica por sus hojas relativamente pequeñas, eglandulares en el pecíolo, con 10–13 pares de nervios laterales, casi indistintos en el haz y elevados en el envés, y sus ráquises y ramas de las inflorescencias, hipantos y lóbulos de los cálices con pubescencia densa color marrón. Además es la única especie hasta el momento conocida en Costa Rica con pétalos densamente pubescentes. En el país se podría comparar *C. polyandra* (Kunth) Rose, pero en está las láminas foliares son blanco lanadas en el envés y generalmente tienen un par de pequeñas glándulas en el ápice del pecíolo (vs. eglandulares) y pétalos glabros (vs. pubescentes). En América Central podría ser similar *C. scottmorii* Prance de Panamá, a razón de los pétalos pubescentes y láminas foliares relativamente pequeñas, pero *C. osaensis* se puede separar fácilmente por las hojas más grandes (6.5–9.0 × 2.5–3.1 vs. 2.5–5 × 1.6–3.0 cm), densamente tomentosa a glabrescentes con tricomas blanquecino-marrón (vs. densamente café aracnoide), e inflorescencias paniculadas (vs. racemosas). En América del Sur, se conocen varias especies con pétalos pubescentes (tabla 1) e inflorescencias paniculadas, pero dentro de este grupo de especies y a razón de las láminas foliares pequeñas y receptáculos completamente cubiertos de pubescencia densa en la superficie exterior, se podría comparar con *C. parvifolia* de Brasil y *C. ulei* de Colombia, Perú, Venezuela, y Brasil. De la primera se puede diferenciar por sus láminas foliares angostas, pecíolos 5.0–7.0 mm de largo y densamente lanado pubescentes (vs. 4.0–5.0 mm y pulverulentos), inflorescencias cortas y poco ramificada, flores con mayor cantidad de estambres (ca. 28 vs. 17–22), y frutos con la superficie del endocarpo granular (vs. fibrosa), además de tener hipantos levemente estriados (vs. sin estrías),

este último carácter también compartido con *C. ulei*. Adicionalmente *C. ulei* difiere de la presente especie por sus láminas foliares elípticas, densamente grisáceo-pubescentes en el envés y con la base redondeada, y por sus flores con ca. 35 estambres.

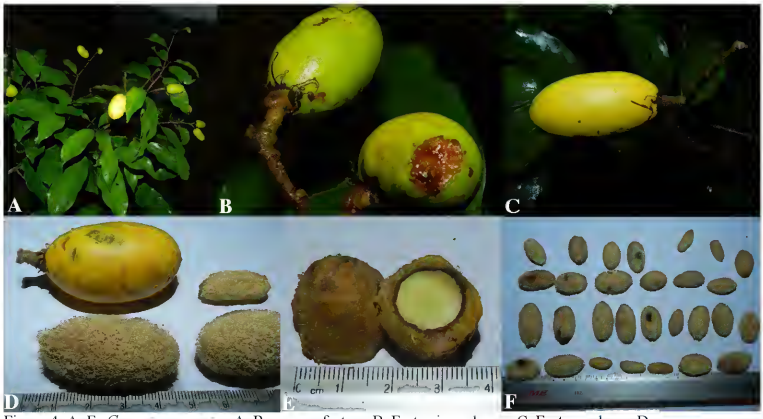

Figura 4. A–F. *Couepia osaensis*. A. Rama con frutos. B. Frutos inmaduros. C. Fruto maduro. D. Comparación del fruto entero y con el mesocarpo removido, nótese la textura fibrosa del endocarpo. E. Corte transversal del fruto. F. Frutos con el mesocarpo removido. (A–F de *R. Aguilar et al 14876*). Fotos por R. Aguilar.

Tabla 1
Especies de *Couepia* con pétalos pubescentes

Especie	Distribución geográfica
Couepia bondarii	Brasil
Couepia cataractae	Brasil
Couepia comosa	Guyana y Venezuela
Couepia eriantha	Colombia, Perú, Bolivia, y Brasil
Couepia grandiflora	Bolivia, Brasil, y Paraguay
Couepia osaensis	Costa Rica
Couepia parvifolia	Brasil
Couepia scottmorii	Panamá
Couepia uiti	Bolivia, Brasil, y Paraguay
Couepia ulei	Colombia, Perú, Venezuela, y Brasil
Couepia venosa	Brasil

Tabla 2
Diferencias entre las especies de *Couepia* en América Central (basado de Prance 2011 online)

Carácteres	*Couepia hondurensis*	*Couepia macrophylla*	*Couepia osaensis*	*Couepia polyandra*	*Couepia scottmorii*
Lámina foliar (cm)	12–19 × 5.5–9.5	19–22 × 6–12	6.5–9.0 × 2.5–3.1	6–13 × 2.5–5.5	2.5–5 × 1.6–3
Tipo infls.	Panícula	Racimo	Panícula	Panícula	Racimo
Pétalos	Glabros	Glabros	Pubescentes	Glabros	Pubescentes
# de estambres	25–30	ca. 280	17–22	11–21	ca. 26
Distribución	Honduras	Panamá, Colombia, Ecuador, Perú y Brasil	Costa Rica	México, Belice, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica y Panamá	Panamá
Altitud (m)	200–300	¿?	216–292	0–600	900–1000

Estudios recientes (Sothers et al. 2014) transfieren *Couepia platycalyx* Cuatrec. a *Licania platycalyx* (Cuatrec.) Sothers & Prance.

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COMPOSITAE OF CENTRAL AMERICA–III. *FLEISCHMANNIA PINNATIFIDA* (EUPATORIEAE), A PINNATIFID-LEAVED NEW SPECIES FROM NICARAGUA

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ABSTRACT

The pinnatifid-leaved new species **Fleischmannia pinnatifida** Pruski (Compositae: Eupatorieae) from Nicaragua is described. *Fleischmannia pinnatifida* and *F. carletonii* are the only pinnatifid-leaved species of the approximately 100 Fleischmannias. *Fleischmanniopsis leucocephala* is vouchered in Nicaragua and *Fleischmanniopsis* is reported as a new generic record for the country.

Recent general identifications of neotropical Compositae include that of a pinnatifid-leaved herbaceous eupatorioid from Nicaragua that has strongly costate-tubed funnelform corollas, low clinanthia, slender anther collars with transversally annulated cell walls, simple glabrous style bases, and stopper-shaped carpopodia. By these technical characters the Nicaraguan plant is positioned within *Fleischmannia* Sch. Bip., where it does not match any previously described species. Nevertheless, the Nicaraguan species has a moderately similar congener in pinnatifid-leaved Honduras-centered *F. carletonii* (B.L. Rob) R.M. King & H. Rob. Although Pruski and Clase (2012) stated that pedate-leaved *F. mayana* Pruski from Belize also "vaguely recalls *F. carletonii*," they acknowledged that the characters in *F. mayana* of obviously campanulate corollas and broad-tipped short anther appendages (viz Pruski & Clase 2012 Figs. 5C, 6A) stretched "the limits of *Fleischmannia*." Subsequently, Robinson and Pruski (2013) excluded *F. mayana* from *Fleischmannia* to *Zyzyura* H. Rob. & Pruski (Eupatorieae). Robinson and Pruski (2013) accepted into *Fleischmannia* only taxa with funnelform corollas and narrower anther appendages, thus returning to the earlier generic concept of *Fleischmannia* used by King and Robinson (1970, 1974, 1975, 1987), Pruski (1997, 2010), Robinson (2001), Robinson and Holmes (2008), and Turner (1997, albeit there as "*Fleischmannia* group of *Eupatorium*"). It is to this more natural concept of *Fleischmannia* that the new species from Nicaragua corresponds, and the plant is described herein as *Fleischmannia pinnatifida* Pruski.

A recent collection of *Fleischmanniopsis leucocephala* (Benth.) R.M. King & H. Rob. (Eupatorieae) marks a new generic record for Nicaragua, and the voucher, typology, and synonymy are given for this species. *Fleischmannia pinnatifida* and *Fleischmanniopsis leucocephala* key in Williams (1976) and Dillon et al. (2001) to a broadly circumscribed *Eupatorium* L.

FLEISCHMANNIA PINNATIFIDA Pruski, **sp. nov.** **TYPE: NICARAGUA. Matagalpa.** 5.2 km NE of Matiguás (N edge) along road to El Congo, Puente Agua Fria, moist forest along stream, 12° 52' 44" N, 85° 25' 43" W, 515 m, 2 Jan 2013, *W.D. Stevens & O.M. Montiel 33819* (holotype: MO: isotype: HULE). Figures 1–4.

Herbae perennes circiter 1 m altae, ramis sparse puberulis, folia opposita petiolata pinnatifida, lamina usque 4 × 2.3 cm supra et subtus glandulosa et sparse puberula, petiolo 0.3–1.8 cm longo; capitulescentia laxe cymosa vel late corymbiforma, capitula discoidea 3.5–4.5 mm longa; flosculi disci 18–23, corollis (2–)2.5–2.7 mm longis infundibuliformis tubo valde costato lobis deltoidea 0.3–0.4 mm longis; styli rami lineari, cypselae 1.4–1.9 mm longae, setae pappo 1.5–2 mm longae

Figure 1– Holotype of *Fleischmannia pinnatifida* (*Stevens & Montiel 33819*, MO)

Figure 2. *Fleischmannia pinnatifida*. A. Pinnatifid leaves. B. Capitulum showing bracteolate peduncle, green phyllaries with narrow tips, pale lavender-blue corollas slightly exserted from the involucre, and linear pale lavender-blue style branches. Photographs taken by Olga Martha Montiel, *Stevens & Montiel 33819*.

Erect perennial herbs ca. 1 m tall; stems subterete to subhexagonal, sparsely and finely puberulent distally with trichomes ca. 0.1 mm long, also sometimes sparsely sessile-glandular in the capitulescence, terminal branchlets filiform. **Leaves** opposite, petiolate, pinnatifid to subbipinnatifid; blade incised to near midrib, triangular-ovate in outline, longer than broad, to 4 × 2.3 cm, primary lobes opposite, usually 2 per side, spreading laterally, lanceolate, to 1–1.5 cm long, well-spaced, sinuses sometimes broad, each lobe often with a single or a pair of lateral lobules or incisions at about midpoint of lobes, lateral lobules usually triangular, mostly 1–3 × 1–2 mm, terminal lobules commonly much longer than lateral lobules, surfaces sessile-glandular and also finely appressed puberulent, blade base mostly cuneate, lobe and lobule margins not serrate, lobes and lobules mostly sharp-tipped; petiole 0.3–1.8 cm long, basically exalate albeit lined with extremely narrow foliar tissue. **Capitulescence** diffusely cymose to openly and broadly corymbiform, 1.5–8 cm diam., held above subtending leaves, branching alternate, branchlets 3–9-capitulate, finely puberulent and sometimes sparsely glandular especially proximally near nodes; peduncles filiform, (3–)6–30 mm long, sparsely puberulent, bracteolate, bracteoles 1–4, spreading or the distal ones subappressed, linear, 0.5–1.5 mm long, setulose or the distal ones subglabrous. **Capitula** discoid, 3.5–4.5 mm long, involucre turbinate to narrowly campanulate, 2–3 mm diam., appearing much broader when pressed; phyllaries lanceolate or the outer most narrowly pyriform, 1.6–4 × 0.3–0.5 mm, weakly subimbricate, ca. 3-seriate, merely moderately graduated with the outer few about half as long as the inner, mostly green, outer phyllaries loosely inserted and sometimes excurrent onto extreme apex of peduncle,

persistent and fully reflexed post fruit, the inner ca. 2 series subequal, subglabrous to puberulent, sometimes glandular, bicostate proximally, margins hyaline or sometimes pinkish, apices acuminate to attenuate; clinanthium flat to weakly convex, epaleate. **Disk florets** 18–23; corolla funnelform, 2.5–2.7 mm long (2–2.5 mm long when dried), slightly exserted from the involucre, pale lavender-blue (as pink on collection label), tube strongly 5-costate, shorter than throat, glabrous, throat only gradually broader than tube, minutely setulose distally, lobes deltate, 0.3–0.4 mm long, setulose and sparsely glandular, the inner surface finely papillose, veins intramarginal; anthers ca. 0.9 mm long, pale, theca base obtuse to rounded and not at all sagittate, apical appendage ovate, ca. 0.17 mm long, longer than wide, apex acute to obtuse, anther collar slender, ca. 0.3 mm long, not wider than filaments, cell walls transversely annular-thickened, endothecial tissue polarized; nectary annular, ca. 0.1 mm tall; style pale lavender-blue, base simple without thickened enlarged node, glabrous, trunk eglandular, glabrous, branches linear, 1.5–1.7 mm long, apical appendage and proximal fertile portions subequal, appendage cylindrical and not at all broadened. **Cypselae** markedly prismatic, 1.4–1.9 mm long, body constricted apically, base gradually narrowed and in the outer florets sometimes curved, faces and costae discolorous, faces concave, black, glabrous to sparsely setulose or pauciglandular apically, costae stramineous, setulose throughout, carpopodium stopper-shaped with well-delineated upper margins obviously broader than narrowed cypselar base, ca. 0.1 mm long, never procurrent onto costate, stramineous; pappus bristles ca. 22, 1.5–2 mm long, usually reaching to near top of corolla throat, capillary, stramineous, scabridulous, nearly contiguous basally, bristle base narrow or only very slightly broadened.

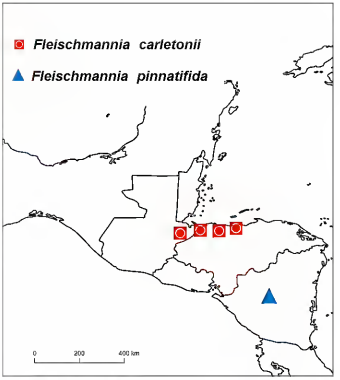

Figure 3. Distributions of *Fleischmannia carletonii* and *Fleischmannia pinnatifida*.

Distribution and ecology. The epipetric rhyacophilous *Fleischmannia pinnatifida* is known only from the type locality near Matiguás, Matagalpa (Fig. 3), which lies in the center of Nicaragua about 130 kilometers northeast of Managua. The type locality is in moist forests along rocky streams at about 515 meters elevation, and this herb is known in bud, flower, and fruit in January.

Figure 4 *Fleischmannia pinnatifida*. A. Pressed capitulum showing apically narrowed phyllaries, inner ca. 2 series of phyllaries subequal and bicostate, and funnelform corollas. B. Adaxial view of post-anthesis anther showing ovate appendage, polarized endothecial tissue, and the slender collar. C. Style showing linear branches with narrow appendages (*Stevens & Montiel 33819*, MO). [Scale bars A. 2 mm, B–C. 0.5 mm]

Fleischmannia pinnatifida, by its divided leaves (whence the epithet), apically narrowed phyllaries, and few small capitula in laxly cymose to openly and broadly corymbiform capitulescences, immediately brings to mind Honduras-centered *F. carletonii*, with these species being the only known pinnatifid-leaved species of *Fleischmannia*, an American genus of about 100 species. Moreover, *F. pinnatifida* and the similar *F. carletonii* share the rhyacophilous habitat preference. Although a few other species from Central America (e.g., *F. capillipes* (Benth.) R.M. King & H. Rob., *F. hammelii* H. Rob., *F. imitans* (B.L. Rob.) R.M. King & H. Rob., *F. sideritidis* (Benth.) R.M. King & H. Rob.) are typically epipetric rhyacophilous herbs having similar diffuse capitulescences, none of these other Fleischmannias have pinnatifid leaves. *Fleischmannia pinnatifida*, as set forth in the key below, differs from *F. carletonii* in foliar details, by sometimes glandular phyllaries, and also by linear (vs. very narrowly clavate) style branches.

Key to *Fleischmannia carletonii* and *Fleischmannia pinnatifida*

1. Herbs 0.2–0.3 m tall, leaves 2–3-pinnatifid, blade about as long as broad, lobes direct forward, distal-most lateral lobules subterminal and mostly subequal to terminal lobule, lobules lanceolate to oblanceolate, 0.5–1.2 mm diam.; phyllaries eglandular, style branches very narrowly clavate; plants of Caribbean drainage Guatemala and northern Honduras ..... **Fleischmannia carletonii**

1. Herbs ca. 1 m tall; leaves pinnatifid to subbipinnatifid, blade longer than broad, lobes spreading laterally, lobules at about midpoint of lobes, terminal lobule commonly much longer than lateral lobules, some lobules triangular, to ca. 2 mm diam.; phyllaries sometimes glandular; style branches linear; plants of central Nicaragua ..... **Fleischmannia pinnatifida**

The report below marks the first occurrence of the *Eupatorium* segregate *Fleischmanniopsis* R.M. King & H. Rob. and of *F. leucocephala* in Nicaragua.

FLEISCHMANNIOPSIS LEUCOCEPHALA (Benth.) R.M. King & H. Rob., Phytologia 21: 403. 1971. *Eupatorium leucocephalum* Benth., Pl. Hartw. 86. 1841. **TYPE: GUATEMALA. Chimaltenango**. In aggeribus, Acatenango, 1840, *Hartweg 588* (isotypes: NY-2).

Eupatorium leucocephalum var. *anodontum* B.L. Rob., *Fleischmanniopsis leucocephala* var. *anodonta* (B.L. Rob.) R.M. King & H. Rob.

Voucher. **NICARAGUA. Nueva Segovia.** Cerro Mogotón, SE slope, along Caño El Cipresal, 13° 44' 52" N, 86° 23' 09" W, 1475 m, 16 Apr 2013, *Stevens & Montiel 34244* (MO).

Although *Fleischmanniopsis*, a genus of about five mid-elevational neotropical species, was named for its similarity in some technical features to *Fleischmannia* (King & Robinson 1971), *Fleischmanniopsis* lacks prominent costae on their corolla tubes that are so characteristic of *Fleischmannia*. A very striking character of showy white phyllaries, however, occurs in three species of *Fleischmanniopsis*, and of these species the widespread *F. leucocephala* is often used in floral displays.

Fleischmanniopsis leucocephala occurs from Veracruz southeastwards into El Salvador and Honduras (King & Robinson 1987; Turner 1997), and is vouchered here from a single station in Nicaragua. The locality on Cerro Mogotón lies within two kilometers of the Honduran border and is only about 35 kilometers southeast of Danlí, Honduras. *Fleischmanniopsis leucocephala* is a moderately common shrub with subscandent stems to three meters long and may be recognized by its serrate trinerved leaves, large pluricapitulate and nearly columnar-paniculate capitulescences, straight (never contorted) pappus bristles that are more or less noncontiguous basally, broadly rounded anther appendage apices, obviously clavate style branches, stopper-shaped carpopodia, and most obviously by the characteristic, very showy, white phyllaries.

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ASTRAGALUS MARTINII (FABACEAE), A NEW SPECIES FROM EASTERN SONORA AND WESTERN CHIHUAHUA, MEXICO

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ABSTRACT

A new species, **Astragalus martinii** Spellenb., Van Devender, & Jenkins, is described from the Mesa del Campanero in extreme eastern Sonora and the Sierra Obscura of Chihuahua, Mexico. The free stipules of *A. martinii*, basally fixed pubescence, and fully bilocular ascending pods place the new species with the sect. *Leptocarpi* as delimited by Barneby in 1964. Within that section it uncomfortably settles near subsect. *Parvi*, differing in habit and particularly proportions of the pod. A key is provided to distinguish *A. martinii* from other species of sect. *Leptocarpi* in the mountains of eastern Sonora, and other species in the vicinity of Yécora, Sonora, are mentioned. The name of this new species honors Paul S. Martin, geoscientist at the University of Arizona and a plant explorer of the northern Sierra Madre Occidental.

In the mid-1930s, Howard Scott Gentry explored remote areas in southern Sonora, making extensive plant collections, noting the vegetation and taking photographs, these efforts resulting in his landmark publication about of the vegetation of the region (Gentry 1942). Although his Río Mayo Region extended north to the Yécora area in the Río Yaqui drainage, he only visited Santa Ana in tropical deciduous forest in that area. He barely entered the Sierra Obscura (Gentry used "Sierra Obscura in his 1942 book and on his collection labels; an alternate spelling is "Oscura").

In the spring of 1985 Paul Martin collected an *Astragalus* from the remote Sierra Obscura in west-central Chihuahua, a specimen that was initially identified as *A. gentry* Standl. This appears to be the first collection of the species described herein. Since that time, the completion of Mexico Federal Highway 16 (MEX 16) between Hermosillo, Sonora, and Cd. Chihuahua, Chihuahua, in 1992 provided greater access to the Sierra Madre Occidental. Between 1975 and 1994, numerous plant collections were made in western Chihuahua and eastern Sonora, including the Yécora area, by Raymond M. Turner, Paul S. Martin, and their students and associates, especially Ana L. Reina-Guererro, Mark Fishbein, George M. Ferguson, and Richard S. Felger. These collections were included in a thorough revision of Gentry's 1942 publication (Martin et al. 1998).

In 1995, Ana L. Reina-G. and Tom Van Devender began an intensive survey of the flora of the Municipio de Yécora in eastern Sonora. The Yécora flora, now known to have at least 1773 taxa, is very diverse, reflecting the Madrean Tropical floristic subdivision of the Sierra Madre Occidental (González-E. et al. 2012; Van Devender & Reina-G. 2014). Endemism is high, with 13 species known only from this Municipio (Van Devender & Reina-G. 2014). Shortly thereafter, *Astragalus*

specimens from the Mesa del Campanero were sent to Rupert Barneby at the New York Botanical Garden. Barneby recognized this *Astragalus* as an undescribed species and communicated that to Van Devender. We here describe the new species; specimens will be distributed as cited.

ASTRAGALUS MARTINII R. Spellenberg, T.R. Van Devender, P.D. Jenkins, **sp. nov.** Figures 1–3. **TYPE: MEXICO. Sonora.** Mpio. de Yécora, 1 km W of Puerto de la Cruz on MEX 16, N slope of Mesa del Campanero, 28º 22' 34" N, 109º 02' 13" W, 1840 m elev., common herbaceous perennial on rocky slope, growing with *Astragalus gentryi*, flowers lavender, 30 Mar 1997, *A.L. Reina-G. 97-458* with T.R. Van Devender (holotype: ARIZ; isotypes: MEXU, MO, NMC, NY, US, USON).

Slender, moderately leafy perennial, thinly strigulose with fine, straight, appressed, white or blackish (or mixed) hairs 0.2–0.3 mm long, the herbage green the leaflets glabrous on adaxial surface. ***Stems*** slender, 1–3 dm long, few to many, radiating from the crown of a slender taproot, branched near the crown, otherwise mostly simple, very thinly strigulose, floriferous from below the middle, decumbent spreading, ascending or erect, sometimes shallowly buried for up to 1 dm (then specimens appearing more or less rhizomatous). ***Stipules*** narrowly triangular to ovate, semi-amplexical, membranous, pale green, 2–3.5 mm long, sparsely strigose on adaxial surface, the margins often more or less ciliate. ***Leaves*** (1.5–)3–10 cm long, with slender petioles ca. 1/5–1/4 the length of the blade; blade of larger leaves with 15–23 obovate or oval to narrowly obovate, elliptic, or oblong, truncate-emarginate or rounded, flat, thin-textured leaflets 2–10 mm long, glabrous on adaxial surface, strigulose abaxially. ***Peduncles*** slender, erect or ascending, straight or a little incurved, 2–10 cm long. ***Racemes*** densely to moderately loosely (1–)6–11-flowered, the flowers spreading to widely ascending, the axis 3–15 mm long in flower, about the same in fruit, the short racemes of flowers and fruits often appearing subcapitate. ***Bracts*** membraneous, pale stramineous to pale purplish, lanceolate to triangular, 1.3–2.3 mm long. ***Pedicels*** ascending or arched outward, at anthesis 0.5–1.8 mm long, about the same in fruit. ***Bracteoles*** usually 0, when present 1–2, pallid, linear-lanceolate, 0.5–1.5 mm long. ***Calyx*** 4.5–6.1 mm long, moderately to densely strigulose with black, white, or mixed black and white hairs, the oblique disk 0.8–1.1 mm deep, the membranous greenish or purplish, deeply campanulate or subcylindric tube 2.5–4 mm long, 1.6–2.3 mm in diameter, the linear-lanceolate to narrowly triangular, subherbaceous teeth 1.6–2.3 mm long, the whole becoming papery-membraneous, ruptured, persistent around base of pod. ***Flowers*** 7.5–10 mm long. ***Petals*** purple at tips, whitish or pale lilac basally. ***Banner*** recurved through 60–90º, claw 3.8–4.2 mm long, blade broadly ovate, 6.1–7 mm long, 5–5.5 mm wide, rounded across the apex except for a shallow notch at tip. ***Wings*** claw 3.5–4.9 mm long, blade obliquely ovoid, 5.0–5.6 mm long, 1.6–2.5 mm wide, gently incurved through 25–30º, margin entire, tip rounded. ***Keel*** (0.8–1 mm shorter than wings) 6.5–8.2 mm long, claws 3.4–4 mm long, blade 3.4–4.2 mm long, 1.9 mm wide, the half ovate blades incurved through 90º to the obtuse, widely acute tip. ***Anthers*** 0.3–0.4 mm long. ***Ovules*** 19–26. ***Pods*** sessile, semi-persistent, in dense clusters as wide or wider than long at the tips of the peduncles, often humistrate; pod as viewed from ventral surface broadly lance-ovoid in outline, as viewed from the side slightly incurved to incurved through about 1/5 of a circle, 9–12 mm long, 4.5–6.5 mm wide, about twice as broad as deep, rounded at base, distally contracted into a short, triangular-cuspidate apex, broadly and bluntly triquetrous, obtusely low-carinate by the thick ventral suture, the lateral faces deeply convex, the dorsal face moderately open-sulcate, the finely strigulose subcoriacous valves green, becoming stramineous, and later blackish, when dry finely transverse rugulose, inflexed as a complete septum about 1.1 mm wide; dehiscence tardy, perhaps occurring on the ground, beginning at the apex. ***Seeds*** brown, dull or slightly lustrous, slightly wrinkled. 1.3–1.7 mm long.

All of the collections of *Astragalus martinii* are from pine-oak forest. At the type locality west of Puerto de la Cruz on the northern slopes of Mesa del Campanero, at 1840 meters elevation, the pine-oak forest on steep rocky slopes is very diverse, dominated by *Pinus engelmanni* and

Quercus arizonica. Most of the paratypes are from flatter areas at 1900 to 2195 meters on top of Mesa del Campanero. In this area, pine-oak forest includes *P. strobiformis* and *Q. jonesii*. Beginning in the 1950s, large areas of pine-oak forest were cleared for apple and other fruit orchards (Rubén Coronado, pers. comm., 2007). *Astragalus martinii* mostly occurs in clayey soil on relatively flat rocky surfaces formed by weathered Oligocene basalt but also was found on disturbed roadsides and in a plowed cornfield near the village of Campanero. It was also found on rocky slopes in mesic pine-oak forest with *Abies durangensis* in Barranca El Salto on the western edge of Mesa del Campanero. In general, *Astragalus martinii* is known to occur between 1800 and 2200 meters elevation.

Figure 1 Holotype of *Astragalus martinii* (*Reina-G. 97-458* et al., ARIZ)

Figure 2. Comparatively large, open form of *Astragalus martini* (*Reina-G. 99-703* et al., ARIZ)

Figure 3 Comparatively small, tufted form of *Astragalus martini* (*Van Devender 95-342* and Reina-G , NMC)

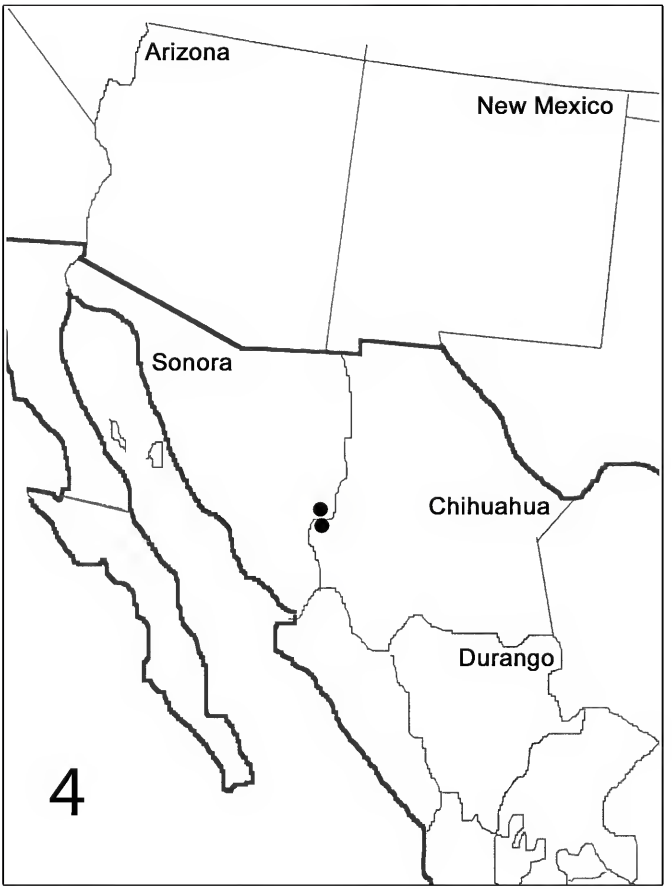

Figure 4. Map of northwestern Mexico and southwestern United States, dots indicating known distribution of *A. martini*. More northerly dot represents Mesa del Campanero, the more southerly dot the Sierra Obscura.

Astragalus martinii has two morphological extremes on Mesa del Campanero. Some plants are green, and large, with slightly larger pods and flowers in comparison to the other extreme, which consists of plants that are comparatively low, densely tufted, and grayish with denser pubescence, the flowers and pods averaging smaller. These phases may be ecologically induced, the smaller, more tufted phase recorded as being in the open, along roads, or in flat ponderosa pine forest. The type is more or less in the middle of the range of variation, being fairly large, green, and leafy, while at the same time fairly densely tufted. In the specimens citations we have noted which form the particular collection represents if it seems extreme by indicating "large, open" and "small, tufted."

Additional specimens examined. **Chihuahua. [Mpio. de Moris]**, Sierra Obscura, under pines, 2000 m, 28° 00' 40" N, 109° 01' 00" W, 26 Mar 1985, *Martin s.n.* (ARIZ). **Sonora. Mpio. de Yécora**: Between El Llano and Campanero, Mesa del Campanero, W of Yécora, 28° 20' 15" N, 109° 01' 15" W, 2100 m, 10 Mar. 1996, *Reina-G. 96-32* (ARIZ, MEXU) (small, tufted); N end of Mesa del Campanero; pine-oak forest, 28° 21' 33" N, 109° 01' 42" W, 2140 m, common herbaceous perennial in shady understory, flowers lavender, some very light, 18 Sep 1999, *Retna-G. 99-703* (ARIZ, MEXU) (large, ± open); ca. 6 air km WSW of Yécora on N end of Mesa del Campanero, 28° 22.17' N, 109° 01.82" W, 2195 m, igneous rock and soil in pine, juniper, and oak woods, 16 Aug 1998, *Spellenberg, Brouillet, & Todsen 12644* (MEXU, NMC, NY); Mesa del Campanero, 1 km N of El Llano along road to MEX 16, 28° 20' 44" N, 109° 01' 42" W, ca. 2100 m, open area on a level mesa in pine-oak woodland, 26 May 1996, *Steinmann 868* (ARIZ, NMC) (small, tufted); Mesa del Campanero, W of Yécora, 28° 21' 30" N, 109° 01' 45" W, 2120 m, pine-oak forest, 1 May 1995, *Van Devender 95-342* (ARIZ, ASU, NMC, RSA, TEX) (small, tufted); Mesa el Campanero, pine-oak forest, 28° 21' 36" N, 109° 01' 36" W; 2100 m, canyon bottom, 6 Sep 1996, *Van Devender 96-384* (NMC, UC, USON) (large, ± open); Mesa el Campanero, pine-oak forest, 28° 21' 36" N, 109° 01' 36" W, 2100 m, roadside, 6 Sep 1996, *Van Devender 96-38* (ARIZ, CIIDIR, RSA) (large, ± open); Mesa del Campanero, Arroyo Largo at head of Barranca El Salto, pine-oak forest, 28° 20' 44" N, 109° 01' 30" W, 2000 m, arroyo bottom, 6 Sept 1996, *Van Devender 96-427* (ARIZ, NMC); El Llano, Mesa del Campanero, 10 km (by air) WSW of Yécora, 28° 20' 28" N, 109° 01' 54" W, 2100 m, open heavily grazed area, 14 Mar 2000, *Van Devender 2000-149* (NMC) (small, tufted); N end of Mesa del Campanero, pine-oak forest, 28° 21' 33" N, 109° 01' 42" W, 2140 m, 5 Apr 2000, *Van Devender 2000-214* (ARIZ) (small, tufted); Barranca El Salto, Mesa del Campanero; pine-oak forest, 28° 21' 18" N, 109° 01' 28" W, 1900 m, locally common perennial herb on rocky slope, flowers light purple (most not yet in flower), 23 Jul 2005, *Van Devender 2005-1139* (NMC); Omar Fraijo's cornfield near Campanero on Mesa del Campanero (W of Yécora), pine-oak forest, 28° 20' 39" N, 109° 01' 22" W, 2115 m, common perennial herb in understory and tree wells in orchard, flowers lavender-pink, 26 Jun 2007, *Van Devender 2007-638* (MO, NMC); Barranca El Salto, Mesa del Campanero; pine-oak forest; 28° 21' 18" N, 109° 01' 48" W, 1900 m, locally very common perennial herb on rocky slope; flowers pink (most plants not reproductive), 7 Oct 2007, *Van Devender* 2007-1020 (ARIZ, ASU, DES, MEXU, MO, NMC, NY, TEX, USON, US) (large, ± open); Mesa del Campanero, upper tributary of Barranca El Salto, 28° 21' 18" N, 109° 01' 48" W, 2000 m, pine-oak forest, 9 Sep 1995, *Wiens 95-017* (ARIZ, NY); Mesa el Campanero, Arroyo largo, upper tributary of Barranca El Salto; 28° 21 ½' N, 109° 02' W, 2080 m, arroyo bottom in pine-oak forest with *Juniperus, Arbutus xalapensis, Quercus durifolia, Astranthium, Cologania, Ranunculus hydrocharoides, Prunella, Cheilanthes hirsuta*, 9 Sep 1995, *Wiens et al. s.n.* (ARIZ).

The late Paul S. Martin (1928-2010) was a geoscientist at the University of Arizona. Among other endeavors, he was known for his hypothesis of human-induced Pleistocene extinction of large mammals in North America. Paul was also deeply interested in the flora and its composition in the northern Sierra Madre Occidental. Therefore, we name this *Astragalus* in recognition of his pioneering contributions to our knowledge of the biota of this region. Though stricken with polio as a young man and walking with one or two canes he, nevertheless, continued field work in remote regions throughout his career. Each of us authors and numerous other individuals have fond memories of one or more field trips led by him. In March 1975, he led an expedition from the University of Arizona to cross the Sierra Madre Occidental through Yécora to the Cascada de Basaseáchi in Chihuahua long before the completion of Mexico Hwy 16 in 1992. He inspired Deborah E. Goldberg to do her dissertation on the vegetation and flora of hydrothermally altered soils on gossans near Santa Ana in 1975-1977 and 1980 (Goldberg 1982). He visited Mesa del Campanero with George M. Ferguson in 1988, 1990, and 1992. He introduced Yécora to Mark Fishbein. Botanical collections made by him and associates were incorporated into the 1998 Gentry's Río Mayo Flora book (Martin et al. 1998).

For North American *Astragalus*, Barneby (1964) constructed a classification with informal phalanxes, wherein he associated species further in formal sections and subsections. Most, if not all, his subsections were new and were described around those species included within. *Astragalus martinii* easily keys to the sect. *Leptocarpi*, but there its identification stalls, its comparatively broad, tardily dehiscent pod preventing easy association with the subsections Barneby constructed. The nature and timing of dehiscence of the pod still is not known but probably occurs on the ground. Pods may be retained on the usually humistrate raceme until well blackened, but on some specimens they may be dislodged fairly easily. If they are ultimately deciduous and dehisce once detached, this precludes the inclusion of *A. martinii* into sect. *Coahuilani*, which has truly persistent pods that dehisce on the raceme. With its relative deep calyx tube, *A. martinii* resembles species in sect. *Pringleani*, where the short, broad pod differs from the usually linear, narrow pods of four species in that section. The pod is more characteristic of sect. *Parvi*. At this time we do not include *A. martinii* in any subsections as constructed by Barneby, but we do believe it belongs within sect. *Leptocarpi*.

The following key distinguishes *Astragalus martinii* from other members of the section *Leptocarpi* that are known to occur above the desert in eastern Sonora (adapted from Barneby 1964).

1. Plants annual, germinating either in fall, winter, or spring, but truly monocarpic, perishing after fruiting ..... **Astragalus nuttallianus** (Nutt.) A. DC.
1. Plants perennial, sometimes short-lived, or biennial, often flowering the first season but not truly monocarpic (nearly always some aged plants in population).

2. Pubescence dolabriform ..... **Astragalus arizonicus** A. Gray
2. Pubescence basifixed.

3. Pods relatively broad, 1/3–½ as broad as long; keel broadly acute or bluntly deltoid.

4. Inflorescences densely compact, 1–1.5 cm long, about as wide, appearing shaggy-hairy because of the densely strigulose-villous calyces; pods shaggy strigulose-villose, stramineous when fully mature ..... **Astragalus hypoxylus** S. Wats.
4. Inflorescence compact, sometimes loosely so, 1.5–3 cm long, often longer than wide, not appearing shaggy-hairy; pods minutely strigulose, black when full mature ..... **Astragalus martinii** Spellenb., Van Devender, & Jenkins

3. Pod relatively narrow, 1/5 as wide as long or narrower; keel tip triangular-acute to subulate and forming an erect to strongly porrect beak.

5. Petals irregularly graduated, the triangular-acute keel-tip surpassing the wings by 0.2–0.8 mm, the shallowly lobed wing-blades relatively short (4–5 mm long) and broad ..... **Astragalus gentryi** Standl.
5. Petals regularly graduated, the keel shorter than the wings and with an erect or porrect beak ..... **Astragalus nothoxys** A. Gray

***Astragali* of Yécora**

Small *Astragalus* were collected all along MEX 16 in the Municipio de Yécora. *Astragalus gentryi* is widespread from 650 meters elevation in tropical deciduous forest to 1860 meters in pine-oak forest but mostly occurs below *A. martinii*. *Astragalus hypoxylus* was found in oak woodland and pine-oak forest at 1500 to 1840 meters elevation south of Maycoba, in Yécora, and just west of Puerto de la Cruz, the latter locality very close to the type locality of *A. martinii*. These records for *A. hypoxylus* in the Sierra Madre Occidental are interesting because it was thought to be a rare endemic in Cochise and Santa Cruz counties, Arizona, 370 km to the north-northwest (Barneby 1964) and is a Species of Concern for the U.S. Fish and Wildlife Service. *Astragalus nothoxys* was found at 1460 to

1540 meters at Maycoba, Yécora, and La Palmita, mostly in oak woodland. Thus, four species of tufted *Astragalus* and the larger white-flowered *A. longissimus* (sect. *Strigulosi*) occur in montane woodlands and forests in the Yécora area. The annual *A. nuttallianus* var. *austrinus* was found at 490 meters elevation in foothills thornscrub at Curea.

ACKNOWLEDGEMENTS

When the description of a new species has taken 2.5 decades to appear from an area once remote but now with increasing botanical exploration because of easier access, some explanation seems in order. During that time key players have changed employment or retired, the major herbarium involved with the species was moved, and series of unmounted, unlabelled specimens were squirreled away, seemingly undiscoverable even by those working with the taxon. We sincerely thank the good work of Sarah Hunkins, Shelly McMahon, Ben Brandt, and George Ferguson, all of ARIZ, for finding much of the "lost" material cited in this paper and helping us with distribution of specimens. We appreciate Rupert Barneby's early comments, where he believed that Van Devender and his colleagues had, indeed, discovered a new species of *Astragalus*. Ana L. Reina-Guerrero, wife of Tom Van Devender, introduced him to Yécora in 1994, beginning a dozen years of rewarding plant exploration and discovery.

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RELATIONSHIPS AND TAXONOMY OF *IPOMOEA VARIABILIS* (CONVOLVULACEAE)

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ABSTRACT

Since at least the early 1900s, two species of *Ipomoea* have been confused—*I. variabilis* (Schltdl. & Cham.) Choisy and *I. mitchellae* Standl. Since Homer D. House considered *I. variabilis* to be a member of *Ipomoea* sect. *Pharbitis,* many subsequent students of the family have followed that disposition. We were able to study the types of both names and discovered that the disposition by House and others is incorrect. *Ipomoea variabilis* is a synonym of *I. batatas* (L.) Lam. and the correct name for specimens that have been identified conventionally as *I. variabilis* should be recognized as *I. mitchellae* of *Ipomoea* ser. *Exogontum.* We discuss the misunderstanding, cite protologues, list types, and indicate the proper relationships of these two species based on both morphological and molecular genetic studies.

House (1908:207) used the name *Ipomoea variabilis* (Schltdl. & Cham.) Choisy for plants with "sepals 3–5 mm wide x 14–18 mm long, hirsute with spreading hairs at the base and corollas 5–6 cm long," and described the flowers as blue or purple. Although House cited the correct synonymy, it is clear he did not compare his plants with the original description of *Convolvulus variabilis* or with Choisy's combination in *Ipomoea.* Schlechtendal and Chamisso (1830: 117) clearly stated that the plants have "sepala elliptica, breviter mucronato-acuminata ... Corolla magna, rosea, 1.5 poll. fere longa (sepals elliptic, short mucronate-acuminate ... Corolla large, pink, usually 1.5 inches long). Choisy (1845:383) quoted Schlechtendal and Chamisso (1830) almost verbatim. House (1908: 207) also cited Hallier (1899: 411) but ignored the fact that Hallier had placed *I. variabilis* in "§ Batatas," which he conceived in a strict sense at that point in time, which is consistent with our modern concept of the sweet potato complex [*Ipomoea* ser. *Batatas* (Choisy) D.F. Austin]. Instead, House placed *I. variabilis* in *Ipomoea* subsect. *Tyrianthinae* within sect. *Pharbitis,* owing ostensibly to the hirsute and spreading hairs at the base of his specimen's sepals (Mexico: Veracruz. Ano 1853, *F. Müller s.n.* NY!), a feature that is decidedly inconsistent with the type of *Convolvulus variabilis* Choisy.

When McDonald (1994) published the Convolvulaceae for the *Flora de Veracruz,* one of the few types that he did not see was that of *Convolvulus variabilis.* At that time, McDonald assumed the holotype was in LE, where Chamisso's types are located, but travel options and political conditions did not allow for a visit to the herbarium. It is now clear that many of the types used by Schlechtendal and Chamisso are in the herbarium at Martin Luther University of Halle-Wittenberg (HAL), where Schlechtendal was professor of botany and director of the Botanical Gardens from

1833 until his death in 1866 (Hoffmann 1998; Kesting & Hoffmann 2000; Meyers Konversations-lexikon 1885-1892:504; Rainer 2003).

McDonald adopted the name *Ipomoea variabilis* on the basis of Homer House's perceptions and description of the binomial, as well as those of Standley and Williams (1970: 39), who demoted the name to varietal status in a broad concept of *Ipomoea indica* (Burm.) Merr., a member of *Ipomoea* ser. *Pharbitis* (Choisy) Benth. Following McDonald's (1994: 129) interpretation, we have used the binomial *I. variabilis* (Austin et al. 2012: 314; Felger et al. 2012: 500). Most specimens in herbaria are now annotated with that name.

George Staples recently pointed out to us that an image of *Convolvulus variabilis* at HAL is now available at Global Plants (2014). We have examined the image of that sheet, annotated by both Chamisso and Schlechtendal, and now realize that Choisy (1845: 383) and Hallier (1899: 411) were correct in aligning the species in *Ipomoea* series *Batatas*. Our previous interpretation of the binomial *I. variabilis* as a plant similar to *I. indica* (Burm.) Merr. is incorrect, because the isotype is actually *I. batatas* (L.) Lam.

Below we provide the proper names and relationships for the two species that have been misinterpreted by many people, including us.

1. **Ipomoea mitchellae** Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 39. 1930. **TYPE: HONDURAS.** Atlántida: wet thicket, La Fragua, alt. 20 m, 7 Dec. 1927, *Standley 52658* (holotype: F0054855F!; isotype: US00111423!).

While this species is widely distributed in Mesoamerica, from Veracruz and Oaxaca, Mexico south to Costa Rica (Austin et al. 2012: 314; Hammel 2010: 112), this is the oldest name available for this distinctive taxon. Austin long interpreted these plants as part of a variable *Ipomoea indica* (Austin 1986: 358, Austin & Huáman 1996: 37), much as Standley and Williams (1970) and many other curators. Although Standley was wrong in suggesting *I. mitchellae* was allied with *I. purpurea* (L.) Lam., he was correct in recognizing this species' close affinities with *I. meyeri* (Spreng.) G. Don. Superficially, *I. mitchellae* and *I. meyeri* are both similar to *I. indica* and other members of *Ipomoea* ser. *Pharbitis*, but that is due to convergence in sepal morphology. Independent phylogenetic analyses indicate these sister species are nested within *Ipomoea* sect. *Exogonium* (McDonald & Mabry 1992: 252; McDonald et al. 2011: 168).

2. **Ipomoea batatas** (L.) Lam., Tabl. Encycl. 1: 465. 1793.
Convolvulus variabilis Schltdl. & Cham., Linnaea 5: 116. 1830. *Ipomoea variabilis* (Schltdl. & Cham.) Choisy in DC., Prodr. 9: 383. 1845. *Ipomoea indica* var. *variabilis* (Schltdl. & Cham.) L.O. Williams, Fieldiana, Botany 32: 191. 1970. **TYPE: MEXICO. Veracruz.** Hacienda de la Laguna, *Schiede & Deppe s.n.* "219" [1828-09] (holotype: HAL0037741 digital image!; isotype?: LE, n.v., cf. Stafleu et al. 1976: 482).

When Choisy (1845: 383) made the combination with *Ipomoea* he cited the basionym and ended the treatment with a dagger symbol (†). It is not clear if that symbol was used to mean that he had not seen original material or if he thought it had been destroyed. Probably, he meant that he was using only the protologue and saw no specimens. He commented that the species was "*Affinis I. ramoni*," which is now regarded as a synonym of *I. trifida* (Kunth) G. Don (*Ipomoea* series *Batatas*). In that suggestion, Choisy was correct.

After Hallier (1899: 411), Carlos O'Donell was one of few modern botanists to correctly maintain *Ipomoea variabilis* in the Batatas complex. O'Donell annotated the holotype of *I. purpusii* House (*Purpus 2213*, NY!) as *I. variabilis* in 1950. Subsequently, Rosangela Simão-Bianchini saw

the sheet in 1996 and annotated it as *I. batatas*. After having seen the type of *C. variabilis* in HAL, we now realize that both annotations are correct, but *I. batatas* has priority.

However, these plants are not the well known hexaploid *Ipomoea batatas* of cultivation but are the long misunderstood tetraploid wild relatives of the crop. Paul Standley, for example, consistently misidentified specimens of the tetraploid as *I. triloba* L. (cf. comments in Austin 1978: 128). That tetraploid variant has been discussed by Austin et al. (1993) and Bohac et al. (1993).

Figure 1. Segment of the type specimen of *Ipomoea variabilis* at HAL showing the sepals and corolla base. Note ovate-mucronate sepal apices and dense pubescence.

Figure 2. Segment of type specimen of *Ipomoea mitchellae* at F, showing the sepals. Note the elongate, acuminate sepals with spreading pubescence.

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WASHINGTONIA × *FILIBUSTA* (ARECACEAE: CORYPHOIDEAE), A NEW HYBRID FROM CULTIVATION

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ABSTRACT

Washingtonia × *filibusta*, a hybrid between *W. filifera* H. Wendl. and *W. robusta* H. Wendl., is named and described from a cultivated plant in Indio, California. *Washingtonia filifera* (California fan palm) and *W. robusta* (Mexican fan palm) have long been cultivated and are especially common landscape subjects in California, western Arizona, and southern Nevada as well as other regions with a suitable climate. They frequently grow side-by-side in landscape settings, providing ample opportunity for hybridization. Hybrid plants are intermediate between the parents and for the past 30 years have become common subjects in the nursery and landscape trade, where they are recognized for their different appearance and cultivation requirements.

Washingtonia × filibusta Hort. ex Hodel, **sp. hyb. nov.** (*W. filifera* H. Wendl. × *W. robusta* H. Wendl.). **TYPE: CULTIVATED. USA. California.** Riverside Co.: Indio, Desert Trace Way, 100 m W of Jackson Street, 1 m elev., 33° 44' 56.31" N, 116° 13' 02.23" W, 13 Jun 2014, *D.R. Hodel 2040* with K. Greby (holotype: BH).

Similar and intermediate to both its parents. Differing from *W. filifera* in its more slender stem; smaller, denser leaf canopy; smaller, brighter green leaves with a small patch of white tomentum abaxially at petiole and blade junction; and shorter inflorescences. Differing from *W. robusta* in its more robust stem not abruptly flared at the base; larger, more expansive canopy; larger, but lighter, medium green leaves; and longer inflorescences. Figures 1–4.

Tree palms, solitary, to 20 m tall (Fig. 1). **Stem** erect, straight, 30–50 cm DBH, slightly flared at base, typically covered with persistent, brownish leaf bases to give rough appearance or if these are removed then smooth, brown, with vertical fissures. **Leaves** ca. 40, palmate, induplicate, erect to spreading to drooping, medium green (Fig. 1); petiole 125 cm long, 14 cm wide at base, 5.75 cm wide at apex, abaxially convex with tinge of burgundy color toward base and moderately covered with whitish, scale-like hairs throughout, adaxially slightly concave or flat and glabrous, margins sharp and with orange-brown, curved teeth 1.25 cm long especially toward base, few, tan, coarse fibers to 8 cm long at base; blade 160 cm long, 180 cm wide, split to ca. 30% in middle, 50% laterally, and 90% at base into 80 segments, the middle the longest, these 125 × 7 cm, lateral 117 × 5 cm, basal 91 × 2 cm, free tips pendulous, hastula 12.5 cm long, narrowly triangular, green, abaxially petiole extending into blade 12.5 cm, narrowly triangular, green with a patch of whitish, felt-like tomentum (Fig. 2), slender, tan filament-like threads at sinuses of adjacent segments especially adaxially. **Inflorescences** ca. 20, interfoliar, to 5 m long (Fig. 1), ascending to spreading for ca. proximal one-third and equaling the subtending leaf and then greatly exceeding this leaf and pendulous in distal two-thirds; base not seen; peduncle at least 125 cm long, ascending to spreading, prophyll at least 40 cm long, 11.5 cm wide, 2-edged, bifid apically, green but tinged with burgundy color toward base, variously covered with woolly to felt-like, tan to whitish tomentum, peduncular bracts 4, green distally, tinged with burgundy color proximally, tips lacerate, brown, variously covered with +/- deciduous, tan to whitish tomentum, most distal bract, ca. 91 cm long with tip split

Figure 1. Type plant of *Washingtonia* × *filibusta*, *Hodel 2040*, Desert Trace Way, Indio, California. © D R Hodel

Figure 2. Abaxial surface of hastula of *Washingtonia* × *filibusta* showing parch of whitish, felt-like tomentum (type, *Hodel 2040*). © D.R Hodel

Figure 3. Flowers of *Washingtonia* × *filibusta* (type, *Hodel 2040*). © D.R Hodel

apically for 15 cm; rachis 150 cm long, sheathed with bracts like those of peduncle, with 4 main branches, the most proximal the longest, this to 370 cm long, with 11 distinct, partial inflorescences or panicles, of these the most proximal is the largest, to 51 cm long, branched to 4 orders, base of inflorescence branches with bracts like those of peduncle, partial inflorescences subtended by tan, thick-papery bracts 81 cm long, 4.5 cm wide; rachillae numerous, slender, 125 mm long, 1 mm diam. cm long. **Flowers** in 2 spiraling rows, ca. 3 mm distant within a row, 8 × 10 mm, white (Fig. 3), on short pedicel 1 mm high; calyx 4 mm high, tubular, 1 mm wide at base, 2 mm wide at apex and shallowly lobed; petals 8 mm long with a slender base 3 mm long and 0.75 mm wide, distal 5 mm conspicuously reflexed and 2 mm wide, thinnish and nearly transparent, tip awl-like, stamens 6, 6 mm long, connate in basal 1 mm and adnate to petals, although shorter than petals the distal portion is conspicuous because of reflexed distal portion of petals, anthers 1.75 mm long; pistil 8 mm long, style slender, 7.5 mm long, conspicuous above stamens and reflexed petals, ovary abruptly flared, 0.5 mm × 1 mm. **Fruits** not seen.

Discussion

Washingtonia filifera from northern Baja California, México, southeastern California, and southwestern Arizona, and *W. robusta* from southern Baja California and western Sonora, México (Bailey 1936; Henderson et al. 1995) have long been cultivated as landscape subjects in the southwestern USA and other regions with a suitable climate. In California in particular, where they are much prized for their ease of culture, fast growth rate, and handsome nature, they are two of the most common ornamental palms and are frequently found growing together, adorning landscapes, streets, gardens, parks, and other public areas.

Over the last 30 years or so growers, landscapers, arborists, horticulturists, and botanists have recognized that intermediate forms between the two species have become common in the nursery trade and landscape. These intermediate forms differ so substantially from either parent in their appearance and, to some extent, their cultivation requirements that growers and landscapers informally coined a name for them, "*filibusta,*" which I have adopted as the epithet for this hybrid species. Table 1 summarizes some of the major differences between *W.* × *filibusta* and its parents. Figure 4 illustrates the three taxa together.

The differences between *Washingtonia* × *filibusta* and its parents can be critical to those who grow and use them in the nursery and landscape trades. Because the palms are frequently and effectively used in homogenous, mass plantings, especially lining streets, boulevards, and other thoroughfares, defining large open spaces, or "softening" buildings or other structures, it is critical to have uniform subjects that differ little or not at all in their appearance. When used in such a manner, the hybrid and its two parent trees are sufficiently different to warrant specifying one taxon while excluding the other two.

Other than their differences in appearance, *Washingtonia* × *filibusta* tends to grow significantly faster than *W. filifera* and as fast as or slightly faster than *W. robusta*. Perhaps most critical, though, is susceptibility to the fungal disease diamond scale, which causes black spotting, chlorosis and necrosis, and premature death of leaves (Hodel 2012). Only *W. filifera* is susceptible to this disease and then only in cooler, moister coastal areas and valleys in California subject to marine influence. It does not attack *W. filifera* in desert areas while *W. robusta* is completely resistant anywhere. Unfortunately, *W.* × *filibusta* is susceptible to diamond scale, with the severity of the disease varying by which parent has a greater influence in the hybrid.

Table 1. Comparison of *Washingtonia filifera*, *W.* × *filibusta*, and *W. robusta*.

	W. filifera	*W.* × *filibusta*	*W. robusta*
Trunk	20 m tall; 50–90 cm DBH, flared only slightly at base.	20–30 m tall; 30–50 cm DBH, flared only slightly at base.	30 m tall; 25–30 cm DBH, abruptly and prominently flared at base.
Canopy	Loose, open.	Moderately loose and open.	Dense, compact
Leaf color	Dull, gray-green or leaden green.	Medium green, only slightly shiny.	Bright, shiny, dark green.
Leaf length (petiole and blade)	3.5–4 m.	2.5–3 m long.	2–2.5 m.
White patch of tomentum abaxial of hastula	Lacking.	Yes.	Yes, prominent.
Inflorescences	Greatly exceeding leaves, 5–6 m long.	Greatly exceeding leaves, 4–5 m long.	Slightly to greatly exceeding leaves, 2.5–4 m long.
Resistance to diamond scale disease	No.	No.	Yes.

Washingtonia × *filibusta* is not an intentionally made hybrid and likely came about inadvertently when growers and others in the nursery trade gathered seeds for propagation of *Washingtonia filifera* and *W. robusta* from cultivated trees. Such seeds were likely the result of hybridization between the two species. Gathering seeds from cultivated trees for propagation of these palms is a typical practice in the nursery trade because the trees are locally common if not abundant and doing so precludes a long and sometimes difficult and arduous and now increasingly illegal trip into desert habitats to collect seeds from wild, natural trees.

The spontaneous hybridization in cultivation shows that there are few or no barriers to hybridization between *Washingtonia filifera* and *W. robusta*. The only barrier to hybridization in wild plants seems to be their geographical isolation. The ranges of the two species do not overlap and in Baja California, where they are closest, there is a several hundred km gap between the northern *W. filifera* and the southern *W. robusta*. Nonetheless, careful exploration of the area north and south of the state line between Baja California Norte and Baja California Sur might prove especially fruitful if *Washingtonia* is discovered in this region and examined for possible hybridization.

Some botanists feel that *Washingtonia* might consist of only one, highly variable species with the two presently accepted and commonly cultivated taxa representing the two extremes, in this case the northerly *W. filifera* and the southerly *W. robusta*. To validate this notion, a judicious and systematic comparison and analysis of *Washingtonia* along the entire length of Baja California would be necessary and perhaps illuminating, looking for populations with a gradation of characters from north to south between the two species. Also, the viability of F2 and/or backcrossed seeds and the fertility of plants so derived presumably might be open to relatively simple observation, since F1 hybrids grow within plantings of otherwise parental individuals. This notion of only one highly variable species might have its origins in an unusual and much visited site at Cataviña near the southerly end of the range of *W. filifera*. Here there are unusually tall specimens of *W. filifera* with unusually slender trunks, this combination leading some to identify them erroneously as *W. robusta*.

Figure 4. *Washingtonia* × *filibusta* (left foreground), *W. robusta* (center), and *W. filifera* (right foreground and left-center background), cultivated at Tyler Ave and S.R. 91, Riverside, California. © D.R. Hodel

Unless growers gather seeds from wild, natural stands or cultivated trees of one species sufficiently isolated to preclude hybridization, *Washingtonia* × *filibusta* will continue to become more common in the landscape, eventually replacing *W. filifera* and *W. robusta*. This trend is of considerable concern in urban areas in the Coachella Valley, such as Palm Springs, where *Washingtonia* × *filibusta* or cultivated *W. robusta* could genetically contaminate nearby wild stands of *W. filifera*.

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AJO PEAK TO TINAJAS ALTAS: A FLORA IN SOUTHWESTERN ARIZONA. PART 7. EUDICOTS: CACTACEAE – CACTUS FAMILY

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ABSTRACT

A floristic account is provided for the cactus family as part of the vascular plant flora of the contiguous protected areas of Organ Pipe Cactus National Monument, Cabeza Prieta National Wildlife Refuge, and the Tinajas Altas Region in the heart of the Sonoran Desert in southwestern Arizona. The modern native cactus flora includes 35 taxa in 12 genera, plus 2 non-native prickly-pears that are not established in the flora area. The overall cactus flora including fossils and non-natives totals 39 taxa in 13 genera: at least 17 taxa are represented by fossils recovered from packrat middens, two of which are no longer present in the flora area. This account includes selected synonyms, English, Spanish, and O'odham common names in when available, identification keys, brief descriptions, images, local and general distributional, natural history, and ethnobotanical information. This flora is specimen-based with selected specimens cited. A new combination is proposed: **Echinocereus coccineus** Engelmann subsp. **santaritensis** (W. Blum & Rutow) M.A. Baker. *Echinomastus erectocentrus* var. *acunensis* is treated as synonym of *Sclerocactus johnsonii*. Club chollas in the flora area previously called *Grusonia kunzei* and *G. parishii* are correctly shown to be *G. wrightiana* and *G. kunzei*, respectively. Cactus diversity in the flora area generally decreases from regions of higher and more predictable rainfall (east side of the flora area) to lower and less predictable rainfall (west side of the flora area). Sixteen taxa generally do not range westward from the flora area and five do not range eastward. *Cylindropuntia*, with 12 present-day taxa, is the most diverse cactus genus in the flora area as well as the Sonoran Desert. Also included is a discussion of convergent evolution of water-conserving adaptations in *Peniocereus striatus* and an African *Euphorbia*. This is the seventh contribution for this flora series published in Phytoneuron and available on the website of the University of Arizona Herbarium.

CACTACEAE – Cactus Family

Cacti, especially organ pipe (*Stenocereus thurberi*), inspired the formation of the Organ Pipe Cactus National Monument. Some cactus species in the present–day flora are defining aspects of the landscape while others can only be seen if you diligently search for them. These cacti have provided people with significant food and beverages, the saguaro and organ pipe fruits being especially delicious and sought after. The local cacti also have been used for house construction, medicine, and for other practical as well as religious or ritual purposes (e.g., Castetter & Bell 1937; Felger 2007). The yellow-spine prickly-pear, *Opuntia engelmannii* var. *flavispina*, occurs at former village and farming sites and may represent introductions and/or selections by Native Americans.

Cactaceae is fourth largest family in the flora area (Felger et al. 2013a & b). The local cactus diversity includes 12 genera and 39 total taxa with 31 native modern species plus 1 hybrid and several varieties (Table 1). At least 18 taxa are represented by fossils recovered from packrat middens. *Coryphantha vivipara* and *Cylindropuntia multigeniculata*, collected by Ice Age packrats in Organ Pipe mountains, are not known from the flora area earlier than 9600 years ago. *Cylindropuntia*, with 12 present-day taxa, is the most diverse cactus genus in the flora area as well as the Sonoran Desert. Organ Pipe has 32 modern, present–day native cactus taxa, Cabeza Prieta has 25 taxa, and 14 occur in the Tinajas Altas region. Two prickly-pears, *Opuntia engelmannii* var. *linguiformis*, which is scarce, and *O. santarita*, which was cultivated, are the only non-native cactus reported in the flora and are not established or reproducing.

Within the study area, the diversity of cactus taxa decreases as aridity increases from east to west. Sixteen taxa do not range westward from the flora area and five do not range eastward (Table 1). For example, the red–flowered mountain hedgehog cactus (*Echinocereus coccineus* subsp. *santaritensis*), typically found in the high mountains of southeastern Arizona, occurs in the flora area only at elevations over 1000 meters in the Ajo Mountains of Organ Pipe, and does not range farther westward. In contrast, the many-headed barrel cactus (*Echinocactus polycephalus*) and beavertail cactus (*Opuntia basilaris* var. *basilaris*) do not range farther eastward in flora area than the hyperarid western part of the region.

Peniocereus striatus and *Lophocereus schottii* are at their northern geographic limits along the southern margin of the flora area and the nearby Tohono O'odham lands—their northern limits due to severity of winter freezing (see Felger et al. 2013a). Five cacti are scarce and/or of limited distribution in the flora area and therefore of local conservation concern: *Lophocereus schottii, Mammillaria thornberi*, *Opuntia engelmannii* var. *flavispina*, *Peniocereus striatus*, and *Sclerocactus johnsonii*. Severe drought, probably correlated with climate change, has impacted a number of local cactus populations, especially *Cylindropuntia leptocaulis*, *C. ramosissima*, *Mammillaria* spp., and *Sclerocactus johnsonii*.

The 37 present-day cacti in the flora area (Figure 1) represent 22% of the total Sonoran Desert cactus flora, which includes about 180 taxa (approximately 128 species plus 27 subspecies and varieties, and 30 hybrids) in 21 genera (Felger et al., unpublished manuscript). Wiggins (1964), in his flora of the Sonoran Desert, included 160 taxa of cactus, of which about 15 percent were infraspecific taxa. The geographic extent used by Wiggins, based loosely on Shreve's (1951) defining map, was considerably broader than newer concepts of the Sonoran Desert (e.g., Felger et al. 2001; Turner & Brown 1982). Furthermore, Wiggins included a number of cactus taxa clearly not even within the boundaries of Shreve's concept of this desert. The cactus family includes about 1800 species in 125 genera, native to the New World with a single exception (Anderson 2001).

Theft of cactus from the flora area is known to occur but the impact on local populations has not been quantified. Poaching is probably greatest along the U.S./Mexico border near Sonoyta and

less common along the more remote public road systems. Some poaching undoubtedly occurs for commercial gain, but some plants are taken for personal collections or medicinal use. Although no formal records of poaching exist, a few instances are remembered. In 2002 a hole and a crumbled cigarette pack were all that remained of a tagged and geo-referenced night-blooming cereus (*Peniocereus greggii*) plant that was part of a monitoring study at Organ Pipe (S. Rutman, pers. observation). In another instance in the early 2000s, a National Parks ranger encountered a man dragging the bottom end of a chain-fruit cholla (*Cylindropuntia fulgida* var. *fulgida*) from Organ Pipe into Mexico, to use as a treatment for a stomach ailment. When asked why he couldn't get the plant in Mexico, the man replied, "Because there are no more left over there." At Bates Well in 2010, two smugglers with an unknown motive were discovered carrying a barrel cactus (*Ferocactus*) pierced by a long iron rod.

Table 1. Local distributions of cactus taxa for the flora in southwestern Arizona. † = modern taxon also represented by a fossil specimen. †† = fossil taxon not found in the modern flora area. ** = non-native and not established (not reproducing) in the flora area. OP = Organ Pipe Cactus National Monument, CP = Cabeza Prieta National Wildlife Refuge, TA = Tinajas Altas Region. Geographic limits: W = taxa generally not ranging westward from the flora area, and E = taxa generally not ranging eastward from the flora area.

Taxon	Region			Geographic limit	
	Organ Pipe	Cabeza Prieta	Tinajas Altas	W	E
†Carnegiea gigantea	OP	CP	TA		
††Coryphantha vivipara	OP				
Cylindropuntia acanthocarpa var. coloradensis	OP	CP	TA		
Cylindropuntia acanthocarpa var. major	OP				
(†Cylindropuntia acanthocarpa)	(OP)		(TA)		
Cylindropuntia acanthocarpa × C. spinosior	OP				
Cylindropuntia arbuscula	OP	CP		W	
†Cylindropuntia bigelovii	OP	CP	TA		
Cylindropuntia echinocarpa		CP	TA		E
Cylindropuntia fulgida var. fulgida	OP	CP		W	
Cylindropuntia fulgida var. mamillata	OP			W	
(†Cylindropuntia cf. fulgida)	(OP)				
†Cylindropuntia leptocaulis	OP	CP			
††Cylindropuntia multigeniculata	OP				
†Cylindropuntia ramosissima	OP	CP	TA		E
Cylindropuntia spinosior	OP	CP		W	
Cylindropuntia versicolor	OP			W	
†Echinocactus polycephalus		CP	TA		E
Echinocereus coccineus ssp. santaritensis	OP			W	
Echinocereus engelmannii ssp. engelmannii	OP	CP	TA		
Echinocereus nicholii	OP	CP		W	
(†Echinocereus sp./spp.)	(OP)		(TA)		
†Ferocactus cylindraceus	OP	CP	TA		
†Ferocactus emoryi	OP	CP		W	

†Ferocactus wislizeni	OP	CP	TA	W	
Grusonia kunzei	OP			W	E
Grusonia wrightiana	OP	CP	TA		
Lophocereus schottii var. schottii	OP	CP		W	
†Mammillaria grahamii	OP	CP	TA		
Mammillaria tetrancistra	OP	CP	TA		
Mammillaria thornberi	OP			W	
(†Mammillaria sp.)			(TA)		
†Opuntia basilaris var. basilaris		CP	TA		E
†Opuntia chlorotica	OP	CP	(†TA)		
Opuntia engelmannii var. engelmannii	OP	CP			
Opuntia engelmannii var. flavispina	OP	CP		W	
**Opuntia engelmannii var. linguiformis	OP				
(†Opuntia engelmannii &/or O. phaeacantha)	(OP)				
Opuntia phaeacantha	OP				
**Opuntia santa-rita	OP				
Peniocereus greggii var. transmontanus	OP	CP	TA	W	
Peniocereus striatus	OP			W	
Sclerocactus johnsonii	OP				
†Stenocereus thurberi	OP	CP		W	
Total taxa: 39	36	25	14	16	5
	Organ Pipe	Cabeza Prieta	Tinajas Altas	West limit	East limit

The first article in this series includes maps and brief descriptions of the physical, biological, ecological, floristic, and deep history of the flora area including references for the fossil record from packrat middens, as well as impacts due to USA–Mexico border issues (Felger et al. 2013a). In the following species accounts, the accepted scientific names are in bold and selected synonyms are italicized within brackets [--]. Common names, when known or worthwhile, are in English, Spanish, and the Hia C-ed O'odham dialect, respectively (see Felger et al. 1992 and 2007 for usage of Hia C-ed O'odham plant names). Spanish-language names are italicized. All specimens cited are at the University of Arizona Herbarium (ARIZ) unless otherwise indicated by the abbreviations for herbaria at Cabeza Prieta National Wildlife Refuge (CAB), Organ Pipe Cactus National Monument (ORPI), and the standardized abbreviations for herbaria (Index Herbariorum, Thiers 2013). Publication information is provided for taxa (accepted names and synonyms) based on type specimens from the flora area or in cases where such information augments our taxonomic decisions. We often refer to Organ Pipe Cactus National Monument as "Organ Pipe," Cabeza Prieta National Wildlife Refuge as "Cabeza Prieta," and the Tinajas Altas Region as "Tinajas Altas." We include only selected natural history and ecological information and references—the literature is far too vast to provide a comprehensive coverage; Drezner and Lazarus (2007) give an excellent overview and interpretation of much of the relevant literature.

We have seen specimens or images of all specimens cited. When no collection number is provided, the specimen is identified by the date of collection. Generally only the first collector's name is given. The two non-native cacti in the flora area are not established as reproducing populations, and are marked with two asterisks (**). Fossil specimens are indicated with a dagger

Figure 1 Flora area in southwestern Arizona (A) Above, overview of regional context, (B) below, detail with local place names. Map B prepared by Ami Pate of Organ Pipe Cactus NM, 2013.

symbol (†). The taxa represented by fossils but no longer present in the flora area are shown with two daggers (††). Area designations are: OP = Organ Pipe Cactus National Monument, CP = Cabeza Prieta National Wildlife Refuge, TA = Tinajas Altas region. Baja California refers to the northern state and Baja California Sur to the southern state of the peninsula, and Baja California Peninsula refers to both states or when the specific state is not known. The identification keys are for the modern flora; taxa no longer occurring in the flora area are not included in the keys.

All Cactaceae are perennials and those in the Dry Borders Region (Felger & Broyles 2007) including southwestern Arizona are characterized as follows: Plants from several centimeters to tree height. Stems very succulent and spiny, or spines absent from *Opuntia basilaris* var. *basilaris*. Branches, spines, leaves, and flowers arise from highly modified short shoots called areoles; areoles on stems or floral structures often bearing extrafloral nectaries. Spines often differentiated into central and radial spines. Leaves absent, or highly reduced and soon deciduous. Flowers sessile, one per areole or multiple flowers in *Lophocereus*. Tepals (perianth segments) usually numerous and intergrading from the outer tepals (sepal-like segments) to the inner tepals (petal-like segments). Stamens numerous. Ovary inferior and deeply embedded in the receptacle, which often bears areoles, spines, scale-like bracts, or is smooth (*Mammillaria*). The proximal part of the receptacle, covering the ovary, is called the pericarpel; the distal part of the receptacle is fused to the hypanthium and the stamens on its inner surface, and is called the floral tube. The base of the floral tube forms a nectar chamber, containing sweet rewards for the pollinators. Fruits succulent or sometimes becoming dry at maturity; seeds numerous.

Nine cactus genera in our flora have extrafloral nectaries (EFNs): *Carnegiea, Cylindropuntia, Echinocactus, Ferocactus, Grusonia, Lophocereus, Opuntia, Sclerocactus,* and *Stenocereus* (e.g., Marazzi et al., unpublished manuscript; also see the species accounts, and Elias 1983 and Pemberton 1988). Whereas floral nectar rewards pollinators, extrafloral nectar rewards ants, which defend the plants aggressively from insects (herbivores) seeking young succulent morsels. The EFNs are located either on the areole "(as modified spines, or the secretory tissue embedded within spines and functional in young stages) or on floral buds (as cryptic EFNs with the secretory tissue apparently embedded within the floral bracts/scales)" (Brigitte Marazzi, pers. com. to Felger, 20 May 2014). *Echinocereus*, *Mammillaria*, and *Peniocereus* are not known to have EFNs.

In the flora area of the northern Sonoran Desert, the funnelform flowers of the two columnar cacti, *Carnegiea* and *Stenocereus*, are pollinated largely by bats, birds, and bees. The two night-blooming cereus (*Peniocereus*) are pollinated by hawk moths. The red-flowered claret-cup cactus (*Echinocereus coccineus*) is adapted for hummingbird pollination and other diurnal-flowering cacti are pollinated primarily by cactus-specialist bees. Some chollas (*Cylindropuntia*) have partially nocturnal flowers and others propagate clonally and generally have sterile flowers. Most cacti have succulent fruits adapted for animal dispersal, and relatively few have fruits that become dry at maturity. The trend for dry fruits is more prominent in the xeric, western reaches of the flora area than in the less arid eastern parts of the flora area. Seven species, or 22% of the cactus in our flora area have fruits that generally become dry at maturity or soon thereafter: *Cylindropuntia acanthocarpa, C. echinocarpa, C. ramosissima, Echinocactus polycephalus, Grusonia kunzei, G. wrightiana*, and *Opuntia basilaris*. However, the fruits of *Cylindropuntia ramosissima* and the two *Grusonia* may be facultatively semi-fleshy with favorable soil moisture.

The identification keys and descriptions pertain to plants and taxa (including genera, species and populations) occurring in the flora area and except where otherwise stated, might not cover variation of taxa or plants in other regions. All photos are by Sue Rutman unless otherwise noted.

Key to the cactus genera of southwestern Arizona

1. Columnar cacti, mature flowering plants 2+ m tall, the stems not constricted into joints or pads.

2. Mature flowering plants usually more than 5 m tall; trunk well developed, branches none or usually arising from more than 2 m above the ground; upper (fertile) stems with 19–25 ribs..... **Carnegiea**
2. Mature flowering plants usually not more than 5 (rarely to 7) m tall; essentially trunkless and much branched from near base; stems with 5–18 (19) ribs.

3. Stem ribs 5–7; stems markedly dimorphic; pericarpel and fruits essentially spineless..... **Lophocereus**
3. Stem ribs (12) 15–18 (19); stems not dimorphic; pericarpel and fruits spiny (spines falling away at maturity)..... **Stenocereus**

1. Not columnar cacti, mature flowering plants usually shorter than 2 m tall, or if taller (some chollas, *Cylindropuntia*) then the stems constricted into many segments or joints.

4. Large barrel cacti, unbranched (solitary), the stem more than 20 cm diameter; larger spines stout and glabrous or with very minute non-overlapping hairs; flowers and fruits hairless .... **Ferocactus**
4. Growth forms various, not large unbranched barrel cacti, the individual stems less than 15 cm diameter (or thick, as in some prickly-pears); spines generally not very thick and rigid (except in *Grusonia* and *Echinocactus*); flowers and fruits.

5. Plants forming dense mounds of multiple stems ("heads") each 9–12 cm thick; spines very stout and rigid, tomentose with overlapping white hairs (use lens); exterior of flowers and fruits copiously white-woolly..... **Echinocactus**
5. Plants not forming dense mounds, the stems mostly less than 7 cm thick and the spines not exceptionally stout and rigid, or if spines stout and rigid, the plants with jointed stems; spine surfaces not covered with short hairs; flowers and fruits not woolly.

6. Chollas and prickly-pears (opuntioids); stems constricted into joints or pads; areoles with glochids (small spines deciduous at a touch; or glochids sometimes absent in *Grusonia*) in addition to the larger persistent spines in at least some areoles (or larger spines none in *O. basilaris*); leaves present on young growth and flowers (pericarpel) but small and quickly deciduous.

7. Prickly-pears; stem segments (cladodes or "pads") flattened or laterally compressed; surfaces relatively flat, not tuberculate; spines not sheathed..... **Opuntia**
7. Chollas; stem segments (cladodes or "joints") more or less rounded in cross-section (cylindroid), often tuberculate; spines sheathed (or the sheaths reduced and inconspicuous in *Grusonia*).

8. Plants often taller than wide; stems with more than 6 joints; spine sheaths covering most or all of each spine (spine sheath perhaps not evident in *C. fulgida* var. *mamillata*)..... **Cylindropuntia**
8. Plants usually forming colonies much wider than tall; stems with 1–6 joints; spine sheaths tiny, only at tip of spine and soon deciduous..... **Grusonia**

6. Not chollas or prickly-pears; stems not constricted into joints or pads; areoles with or without spines but without glochids (if spines small, then not readily deciduous); leaves none.

9. Stems less than 2 cm diameter, more than 20 times longer than wide; spines inconspicuous, 1–8 mm long, not hooked; roots tuberous; rare..... **Peniocereus**

9. Stems 3–9 cm thick (if less than 3 cm then the central spines hooked), less than 10 times as long as wide; spines conspicuous, more than 8 mm long; roots not tuberous.

10. Most areoles with at least one hooked spine; flowers (pericarpel) and fruits without scales or spines …….. **Mammillaria**
10. Spines straight or curved but not hooked; flowers (pericarpel) and fruits with scales or spines.

11. Plants usually branched, mostly from near the base, the stems more than twice as long as thick; flowers and fruits spiny…….. **Echinocereus**
11. Plants usually unbranched, usually less than twice as tall as thick, ovoid to nearly globose; flowers and fruits with scales but not spineless … …... **Sclerocactus**

SPECIES ACCOUNTS

Carnegiea

The genus has a single species. It is the largest cactus north of Mexico.

Carnegiea gigantea (Engelmann) Britton & Rose
[*Cereus giganteus* Engelmann]
Saguaro, sahuaro; saguaro; haːsañ. Figure 2.

Stems unbranched or mostly with several erect branches; stem tissue becoming black when cut or injured (see *Cylindropuntia fulgida* and *Lophocereus*). Stems heteromorphic, the transition from sterile (juvenile) to fertile (mature) growth and first branches often about 4–5 m above ground, the branches fertile (producing flowers). Sterile (lower) stem with 11–15+ ribs, the areoles with stout, rigid spines, the longer central spine (3.7) 5–11 cm × (0.8) 1–2.3 mm; the sterile stem portion becoming the trunk, not bearing flowers (except sometimes near the zone of transition to mature growth), often reaching more than 30 cm diameter and sometimes to 75 cm diameter (Pinkava 1995). Fertile (upper) portion of stems relatively more slender, often 35–53 cm diameter, mostly with 19–25 stem ribs, the ribs shallower than those of the sterile stems, with closely set or nearly confluent flower-bearing areoles, the spines 2–3 cm × 0.3–0.4 mm, flexible and bristle-like.

Flowers often many per rib and mostly crowded, nocturnal, opening a few hours after sunset and usually remaining open until about midday or later depending on temperature. Flowers 8.5–13 × 6.5–8 cm; receptacle narrowly funnelform, with an unusually large region of solid tissue between the ovary and nectar chamber. Larger (inner) tepals 2.3–3.5 × 1.2–1.8 cm; inner tepals, filaments, style, and stigmas white; outer tepals and scales (floral bracts) green and often with reddish tips. Areoles of floral bracts (scales) spineless or sometimes with a few bristle-like spines, and bearing small tufts of wool; floral scales bearing extrafloral nectaries. Flowering mostly late April through much of May and into early June; the first buds and flowers tend to emerge on the east side of stems; "flowers appear all over the stem apex, but are better developed on the east-facing side due to the higher temperatures there (Johnson 1924)" Drezner (2014: 587).

Fruits 6–9.5 × 3.5–4 cm just before dehiscence (opening), ellipsoid to obovoid, mostly green, sometimes red especially near the tip, spineless or sometimes with few, weak, flexible, persistent spines in some or rarely most areoles. (Stunted fruits or those developing under stress seem prone to develop spines.) Dried floral remnant often persistent (the margin of its dilated base can be used like a knife for slicing open the fruit). Fruit rind (pericarpel) bright red inside, not edible, splitting open at maturity into 3 or 4 thick, spreading to recurved lobes, and from a distance appearing like strange red flowers. Fruit pulp juicy, bright red, sweet, and delicious. Seeds about 2 mm diameter, dark red-

brown to blackish, shiny and nearly smooth, and edible. Fruits mostly ripe in June and early July, rarely a few in August.

Figure 2. *Carnegiea gigantea.* (A) Near Kris Eggle Visitor Center, Organ Pipe Cactus National Monument, 4 Feb 2005. (B) Chuckwalla Hills, 19 May 2006. (C) Estes Canyon, 25 May 2005. (D) Ripe fruit, note the persistent dried floral remnant, Hwy 85 at Eagle Pass, 3 Jul 2006. (E) Lesser long-nosed bat (*Leptonycteris curasoae*) covered with *Carnegiea* pollen, Bull Pasture, 15 May 2012; the bat is held in a gloved hand to avoid potential rabies from a bite, photo by Tim Tibbitts. (F) Saguaro ribs, between Chico Shuni Village and Tepee Butte, 4 Feb 2005. (G) Cross-section of a mature stem (from a fallen plant) near Organ Pipe headquarters, 25 Jan 2005. (H) Areoles of a young plant, note the stout spines and bifurcating stem rib, Redondo Valley, north of Why, 20 Jan 2008.

Widespread and common across the region including middle and upper bajadas, hills and all mountains including the Ajo Mountains to over 4100 feet. The Puerto Blanco samples, dated at 10,500 years, are the oldest documented record for saguaros anywhere and probably reflect its arrival in the area. Some older dates for saguaro samples are contaminants (Van Devender 2002).

Sonoran Desert in Arizona and Sonora and ranging southward into thornscrub in southern Sonora, and scarcely extending into California near the Colorado River. The saguaro does not occur naturally on Baja California Peninsula.

This giant columnar cactus is the very symbol of the Sonoran Desert in Arizona and Sonora, where it a keystone species and the state flower of Arizona (e.g., Drezner 2014; Felger 2007). This genus of a single species was named by Britton and Rose, who wrote: "The genus is dedicated to Mr. Andrew Carnegie. The Desert Laboratory of the Carnegie Institution of Washington, at Tucson, Arizona, is surrounded by typical specimens of this unique plant" (1908: 188). The often repeated but unconfirmed story is that, "naming the plant for Carnegie was a ploy to extract further funding from him for plant research," but that he saw through the ploy and was not pleased (Crosswhite 1980: 6).

Saguaros are long-lived and can be truly big—over 10 m tall and up to 9000 kg (Niklas & Buchman 1994). The largest ones, however, are generally not the oldest ones. They often live about 150 years, the maximum life expectancy varying from about 125–200 years. There is considerable variation in maximum size, growth rate, and transition to adult growth (height and age of first flowering and branching), with this variation generally related to gradients in aridity and probably secondarily to local habitat differences (e.g., Drezner 2008, 2013, 2014; Drezner & Lazarus 2008; Steenbergh & Lowe 1983). For example, saguaros in the more arid, western reaches of the flora area probably live longer, commence flowering at a later age (onset of flowering may be more than a century) and generally have fewer branches and achieve smaller maximum sizes than those in the less arid eastern reaches of the flora area.

Saguaro seeds germinate with the summer monsoon (e.g., Steenbergh & Lowe 1969) and begin life in safe sites, generally beneath desert shrubs and trees, often legumes such as ironwood (*Olneya*) and palo verde (*Parkinsonia* spp.). Within the flora area, these nurse plants reduce the likelihood of a frost killing the tender young plants, by reducing heat loss to the night sky. Within the flora area but especially at the colder eastern and northern limits of the saguaro, populations are found on south-facing slopes, and often among boulders that radiate heat collected during the day. Throughout their range, nurse plants and sometimes rocks offer young plants protection from the fantastic sun of a Sonoran summer. "However, sometimes the usual nurse plants are absent, such as at MacDougal Pass and the cactus flat north of Playa Díaz—a sand flat devoid of larger desert shrubs or trees" in northwestern Sonora just south of the southeastern corner of Cabeza Prieta. "In such places *Pleuraphis rigida* [*Hilaria rigida*], a large perennial grass, is the most frequent saguaro nurse plant" (Felger 2000: 205).

The massive saguaro stems have relatively low surface-volume ratios in keeping with the need for water conservation. As with senitas (*Lophocereus schottii*) and many other large columnar cacti, the younger plants have fewer stem ribs, resulting in a lower s/v ratio, while the fertile stems of the larger plants have more stem ribs and a higher s/v ratio (Felger & Henrickson 1997). Cross-section outlines for two sample saguaro fertile stems, 35 and 53 cm diameter, are shown in figure 35. Both stems have 22 ribs and low s/v ratios, ranging from 0.1–0.17 cm^2 per unit volume. The ratios were determined from cross sections. If each stem were a true cylinder, with these diameters the s/v ratios would be smaller still, about 0.07–0.11 cm^2 per unit volume. When these values are compared to the measured s/v ratios, one can see that the ribs have only a minor effect on the s/v ratio in this

large-stemmed cactus. This favorable s/v ratio for water conservation is achieved at the expense of limiting photosynthetic tissue and replacing it with large volumes of non-photosynthetic, water-storing tissue (Drezner 2003; Mauseth 2000; also see discussion for *Peniocereus striatus*).

The abundant flowers and fruits of the saguaro are irresistible to the Sonoran Desert fauna. The lesser long-nosed bat (*Leptonycteris yerbabuenae*) is among the important pollinators and seed dispersers at night along with the western white-winged dove (*Zenaida asiatica mearnsii*) in daytime (e.g., Fleming 2002; Fleming et al. 1996; Martínez del Rio 2007). Numerous other birds, bees and other insects, also visit the flowers, as well as small mammals like round-tailed and Harris antelope ground squirrels (Tim Tibbitts, observation; also see *Stenocereus thurberi*). The fruits are consumed and seeds dispersed by an even wider range of animals, including coyotes, javelinas, lizards, desert tortoises, and birds ranging from ravens to cactus wrens, finches, and orioles. The lesser long-nosed bats feed on floral nectar of saguaros as well as that of organ pipes and agaves (*Agave palmeri*). The agave pollen is large-grained, sticky, and a rich yellow color, imparting a golden-yellow color to the bat's fur. Saguaro pollen by comparison is finer, drier, and paler, imparting a pale blonde color to the bat's fur. However, the saguaro doesn't enjoy a commensal relationship with all its neighbors. Saguaros are sometimes uncommon near waterholes, especially in the Tinajas Altas region, undoubtedly due to the desert bighorn that smash the stems with their horns in order to eat the succulent tissue (Felger et al. 2012; Russo 1956).

The ecologist Forrest Shreve observed, "The sahuaro appears to suffer from very few diseases and natural enemies, the greatest decimation in its numbers being occasioned by mechanical agencies. When struck by lightning or wounded in any other manner during the dry season, it recovers rapidly by the formation of a heavy callus over the wounded spot. If it is wounded in the rainy season, however, bacterial decay sets in very rapidly and a large plant may be destroyed in less than a week as a result of a small wound." (Shreve 1920: 166). Shreve was correct concerning recovery from most dry-season wounds but more hopeful than accurate on the recovery from lightning, which in any case would rarely occur during the dry season. For instance, on 4 September 1969, following a spectacular storm in the Tucson Mountains of Saguaro National Park, Warren Steenbergh surveyed 17.7 ha and found 11 victims of "instant death by explosive mechanical breakage and massive destruction of cell tissues" (Steenbergh 1972). An ongoing study of about 135 reproductive individuals on a 0.96 ha plot adjacent to Saguaro National Park (East) recorded death-by-lightening for three individuals between 1997 and 2014 (William Peachey, pers. comm. to Malusa 2014). Victims are inevitably among the largest individuals—the lightning rods of the desert.

The hot bolts of the summer monsoon are not the only violent agent of mortality for the giant cactus. Blowdown can occur whenever these large, heavy plants are turgid and the soil is wet and relatively soft. At least 60 large saguaros were blown over in a microburst wind and rainstorm one night in August 1992 in the vicinity of Little Tule Well, visible from the road along a distance of about 2 km, and the area of wind-felled giant cacti extended far beyond those two kilometers. Nearly all these saguaros were lying in the same direction with the tips pointing southwest. In addition many large chollas (*Cylindropuntia fulgida* and some *C. bigelovii*) and a few large ocotillos (*Fouquieria splendens*) had blown over. For severe weather events, the winter storm of January 21–22, 2010 was noteworthy. Within view along the South Puerto Blanco Drive, 156 saguaros, 3 organ pipes, and 1 senita cactus fell over as a result of this storm. All except one saguaro were large individuals. Maximum wind speed at the nearby town of Ajo reached 94 mph on January 21 (Bohlin et al. 2010); in the previous 24 hours, 2.5 inches of rain had fallen at the nearby Senita Basin weather station (Organ Pipe Cactus National Monument 2011). A combination of high wind and wet soil was responsible for this blowdown event; higher gusts have been recorded in previous years when the soil was not as wet, without any blowdowns of this magnitude.

The saguaro is the most culturally important and revered plant in the flora region and across the Sonoran Desert in Arizona and northern Sonora (Bell et al. 1980; Booth 2005; Bruhn 1971; Castetter & Bell 1937; Castetter & Underhill 1935; Crosswhite 1980; Felger et al. 1992; Hodgson 2001; Lumholtz 1912; Nabhan 1982, 1985; Nabhan et al. 1982; Rea 1997; Toupal 2006; Betty Melvin in Zepeda 1985: 73). The fruit, ripe in early summer, served as a major food resource, and people seasonally moved their residences for the harvest. Important saguaro fruit-gathering camps for the Hia C'ed O'odham included Ajo, Bates Well, the Quijotoa Mountains, Quitovac, and Santa Rosa (Bell et al. 1980), and some camps were used for harvesting organ pipe fruit as well (Hodgson 2001). The Presidential Proclamation establishing Organ Pipe Cactus National Monument in 1937 specifically allows the O'odham to continue their traditional harvesting of the fruits.

The juicy, sweet pulp is eaten fresh, dried for later use (see organ pipe, *Stenocereus thurberi*), or made into syrup and wine. The protein- and oil-rich seeds are ground and consumed, either freshly harvested or stored. Saguaro and organ pipe wine is ceremonially important among O'odham groups in the Dry Borders region. "They eat [saguaro fruit] and they eat the syrup out of the [saguaro fruit] and jam. . . and seeds. . . they [make gruel with wheat]" (Betty Melvin in Zepeda 1985: 73). Lumholtz (1912: 331) mentioned that Hia Ced O'odham "used to come as far as Quitovaquito and Santo Domingo to gather mezquite beans. . . and eat sahuaro and pitahaya." (Santo Domingo was an hacienda near Quitobaquito along the Río Sonoyta.)

The term *pitahaya* has been used to refer to columnar cacti in general, including the saguaro and organ pipe, as well as *Echinocereus* (Castetter & Underhill 1935; Crosswhite 1980; Felger 2007; Mitch 1972). The 17th century travels of Kino and Manje must have been sustained in part by the dried fruits, for they rarely traveled during the summer yet often mention the pitahaya fruits given to them by the people of Pimería Alta (Burrus 1971). When ripe saguaro fruits open, the red seed-filled pulp may fall from the husk (pericarpel) to dry in branches of nurse trees or on rocky ground. These have been gathered by Tohono O'odham as a sweet treat called *chuñ*. Saguaro fruit dried as fruit leather can be kept for many months, eaten as nutritious trail food, or pressed like figs in "saguaro newton" cookies (Martha Ames Burgess, pers. com. to Felger, 2014; also see Hodgson 2001).

The dry, woody stem ribs were used for construction material—made into slats for house frames, walls, and shelves, and also fashioned into saguaro fruit-gathering poles, light tools, tongs for picking cholla buds and joints, cradleboards, bird cages, traps for quail, and fire drill boards (Bell et al. 1980; Felger 2007; Felger et al. 1992). Cactus "boots," the woody calluses formed around woodpecker or flicker holes, were fashioned into various containers or vessels, including drinking bottles, dishes, and tobacco pouches. Ezell (1937) and Haury (1938/1965) deduced that the Hohokam used vinegar from saguaro wine to etch designs on seashells that are so abundant in the archaeological record.

OP: South Puerto Blanco Drive, 6 km W of Hwy 85, 26 Apr 1990, *Felger 90-70* (ARIZ, ORPI 15309). Upper bajada of Ajo Mts along Alamo Canyon Road, *Rutman 12 Jun 2002* (ORPI 14849). Senita Basin, *Anderson 14 Jun 2002* (ORPI 14848). †Alamo Canyon, seeds, 8130 & 8590 ybp. †Puerto Blanco Mts, on ridge, seeds, from modern (30) to 10,540 ybp (20 samples).

CP: Charlie Bell Road near the E Refuge Boundary, 12 Jun 1992, *Felger 92-532*. 3.1 mi W of Tule Well on Camino del Diablo, 5 Mar 1995, *Rebman 2884* (DES).

TA: See Felger et al. (2012). †Tinajas Altas, seeds, 1230 to 8970 ybp (6 samples). †Butler Mts, seeds, 3820 to 10,500 ybp (4 samples; also to 11,250 ybp, but dates older than 10,500 years may be contaminants).

Cylindropuntia – Cholla; *choya*

Low-growing to shrub-sized cacti (or sometimes small trees). Stem segments (joints or cladodes) cylindrical and longer than wide. Spines uniquely enveloped with a deciduous epidermal sheath. Spine glands as nectaries in the upper part of areoles functioning on young stems, floral buds, and flowers. Flowers diurnal, except crepuscular or nocturnal in *C. fulgida* and *C. leptocaulis*, and *C.*

ramosissima. The genus includes 35 species native in western USA, Mexico, and the West Indies. The greatest diversity is in southwestern USA and adjacent Mexico, and especially the Sonoran Desert region.

The three opuntioid genera (subfamily Opuntioideae) in the flora area, *Cylindropuntia* (chollas), *Grusonia* (club chollas), and *Opuntia* (prickly-pears), are generally characterized as follows: Stems with determinate, rhythmic (seasonal or annual), constricted growth increments resulting in individual stem segments or cladodes (called "joints" in chollas and club chollas, and "pads" in prickly-pears). Areoles bear glochids (small, readily detachable spines with tiny retrorse barbs), and at least some areoles bear spines, which generally are not readily detachable (spines absent on *Opuntia basilaris* var. *basilaris*). Young, growing stem segments and buds and flowers bear small but conspicuous leaves, 1 per areole, succulent, subulate, cylindrical, or conical, and are soon deciduous. These small, vestigial leaves have C_3 photosynthesis, in contrast the rest of the plant and most cacti (including those in the flora area), which have CAM photosynthesis. The stamens are sensitive: the filaments close inward when touched, for example enveloping a pollinating bee. The actual seeds are enclosed in larger, light tan, bony aril-like structures, which look like seeds. This bony aril-like covering of opuntioid seeds forms as flaps along the margins of the curled distal part of the funiculus. The actual seed has a nearly smooth, dark brown testa (seed coat) and a shape much like that of other large cactus seeds, but is fused to the inner surface of the much larger and variously shaped aril-like cover.

Cylindropuntia, with 12 taxa in the floral area, is the most diverse cactus genus in the region as well as in the Sonoran and Chihuahuan Deserts. Chollas are a conspicuous feature of the landscape across the flora area. The chollas of the eastern, or Arizona Upland areas of the flora area have fleshy fruits (except *C. acanthocarpa*), while the "western" species, in the more arid Lower Colorado Desert region, tend to have fruits that quickly become dry upon ripening.

Sue Rutman found many cholla populations significantly reduced during the deep drought in the decade beginning in the early 2000s, including widespread die-off in Organ Pipe and Cabeza Prieta and southward in northwestern Sonora. Not only was the drought significant enough to cause loss of turgidity and mortality, but also small mammals began eating chollas for scarce moisture. The smaller chollas with relatively high surface/volume ratios, such as *C. leptocaulis* and *C. ramosissima*, experienced the greatest die-off. For example, near Teepee Butte in Cabeza Prieta, only a small percentage of *C. ramosissima* remained by about 2010 in an area where the species previously was a major part of the landscape. As of 2014, these populations had not recovered. Similar drought-induced die-off of chollas has been documented in other regions of the Sonoran Desert (Bobich et al. 2014).

Ranchers occasionally burn the spines off both chollas and prickly-pears to make them more palatable for cattle, a process referred to as *chamuscando* (scorching the exterior), which dates back to mid-1700s. For example, Ratcliff (1946) reported that in Organ Pipe, "The Grays have burned cholla cactus to furnish some food for the stock. After the spines have been burned off the cattle eat all edible portions down to the stalk."

Flower buds and young cladodes (joints or stem segments) of the larger chollas were harvested in spring and cooked as vegetables. The fruits of the fleshy or succulent-fruited species were eaten fresh or cooked. The large "seeds" were discarded. The spines and glochids of chollas and prickly-pears were removed by several methods including vigorously brushing them in sand or gravel, often using a creosotebush (*Larrea*) branch as a brush, or soaking in water (e.g., Childs 1954; Felger 2007; Felger & Moser 1985; Hodgson 2001; Rea 1997).

1. Fruits proliferating in perennial pendant chains, not spiny, remaining green and fleshy when ripe, present all year ..... **Cylindropuntia fulgida**
1. Fruits single, not proliferating in pendent chains (occasionally with 2 fruits together), the fruits fleshy and green or yellow, present all year or less, spiny or not, and sometimes becoming dry upon ripening.

2. Main axis (trunk) well developed, generally straight and erect; fruits yellow.

3. Joints (3) 4–6+ cm diameter (excluding spines), and very readily detachable; stem surfaces obscured by a dense cover of spines; inner tepals pale yellow-green; fruits soon becoming dry or sometimes persisting and semi-fleshy ..... **Cylindropuntia bigelovii**
3. Joints less than 3 cm diameter, not readily detachable; stem surfaces generally visible; inner tepals fuchsia to purple; fruits fleshy and persistent. ..... **Cylindropuntia spinosior**

2. Main axis (trunk) not well developed, or if so, then usually not straight and erect; fruits generally not yellow.

4. Joints 1.5 cm or more in diameter, the surfaces visible through a sparse cover of spines or partially to fully obscured by spines, each joint usually evenly spiny from the base to the tip; stems variously purplish, reddish, or greenish.

5. Fruits remaining fleshy at maturity and semi-persistent ……..... **Cylindropuntia versicolor**
5. Fruits dry when mature and not persistent.

6. Stem tubercles mostly 16–24 mm long; inner tepals variable—yellow, orange-brown to dull golden-yellow, red, or purple, the filaments red or red-purple (occasionally green); basal tubercles of fruits much longer than upper tubercles .. **Cylindropuntia acanthocarpa**
6. Stem tubercles 11–16 mm long; inner tepals green; filaments green to yellow; basal tubercles of fruits nearly equal to the upper ones ..... **Cylindropuntia echinocarpa**

4. Joints mostly 1 (1.2) cm or less in diameter, the surfaces readily visible through a sparse cover of spines, the lower areoles of each joint likely to bear only glochids; stems remaining green all year.

7. Tubercles rather flat but sharply defined with diamond-shaped (rhomboid) outlines; each areole in a groove; fruits dry and bristly at maturity..... **Cylindropuntia ramosissima**
7. Tubercles relatively obscure or poorly developed, the stem surfaces smooth; areoles not in grooves; fruits fleshy and not bristly at maturity.

8. Plants usually with a short but thick, woody trunk; terminal joints mostly 7–12 mm diameter; ripe fruits yellow-green or mostly green (sometimes tinged with pink or pale red) .... **Cylindropuntia arbuscula**
8. Plants without a well-defined trunk; joints mostly 4.5–6.5 mm diameter; ripe fruits bright red-orange ..... **Cylindropuntia leptocaulis**

Cylindropuntia acanthocarpa (Engelmann & J.M. Bigelow) F.M. Knuth
[*Opuntia acanthocarpa* Engelmann & J.M. Bigelow, 1856]
Buckhorn cholla; *choya*; ciolim (also called hanamĭ, the general term for cholla). Figures 3 & 4.

Shrubby chollas, 0.4–2 m tall; trunk often poorly defined, not straight; branching at various heights, the branches including the ultimate joints upright to spreading, green to grayish green, and

becoming reddish purple on some plants in winter and dry seasons, while other plants, even adjacent ones, remain green or greenish. Stem segments (joints) firmly attached. Mid-joint stem tubercles 1.5–3 cm long, more than twice as long as broad. Spines moderately to quite densely covering the joints, often partially obscuring stem surfaces; spines highly variable among individual plants, even adjacent ones: spines white, yellow to dark grayish or reddish purple, the spine sheaths yellow and inflated (baggy) to dark in color and tightly fitting (not baggy). Flowers 5–6 cm wide, highly variable in color but uniform on an individual plant: inner tepals uniformly dull to bright yellow, golden-yellow, orange or orange-brown, red–orange or reddish, rose-pink, or sometimes bright red; flowering April and May. Filaments red, or rarely green; anthers yellow. Fruits dry after ripening, generally within one to several months, bur-like with bristly spines, and not persistent, the basal tubercles of fruits much longer than upper tubercles; dry fruits variously tan to purplish black, eventually becoming gray or brownish, or fruits sometimes infertile, tan, and shriveled.

Buckhorn cholla is common and widespread across most of the flora area; sandy to rocky soils on hills and mountains, bajadas, and desert plains and valley flats, from the lowest elevations to the higher mountains. It has been part of the local flora for at least 20,500 years.

Cylindropuntia acanthocarpa occurs in the Sonoran and Mohave Deserts: northwestern Sonora, western and central Arizona, southeastern California, southern Nevada, and southwestern Utah. Populations in northwestern Baja California formerly included in *C. acanthocarpa* have been segregated as *C. sanfelipensis* (Rebman) Rebman. *Cylindropuntia acanthocarpa* is diploid and has bisexual (perfect) flowers, while *C. sanfelipensis* is hexaploid and gynodioecious (Rebman 1995, 1999). There are, however, other gynodioecious chollas.

The flower buds and young stems (cladodes or joints), harvested in spring and often pit-baked, have been important food resource for O'odham people since prehistoric times (Felger 2007; Greenhouse et al. 1981; Hodgson 2001). Seepweed (*Suaeda nigra*) often was used to line the pit and as the interlayered steamer (Curtin 1949; Rea 1997; Russell 1908), or saltbush (*Atriplex* spp., including *A. cansescens*) was used if seepweed was not available (Martha Ames Burgess, pers. comm. to Felger, 2014). Betty Melvin (in Zepeda 1985: 55) related that the Hia Ced O'odham "collected the cholla buds, we'd collect it and dry it." The baked, dried flower buds continue to be a favored food of the regional O'odham people (Hodgson 2001; Rea 1997) and are available in southern Arizona as a gourmet specialty food (Burgess 2014).

Four intergrading varieties *Cylindropuntia acanthocarpa* have been recognized by Benson (1982) and Pinkava (1999a, 2003a), two of which occur in the flora area. Chollas in the flora area called variety *coloradensis* are reported as generally replacing those called var. *major* westward in the Lower Colorado Valley area, encompassing portions of the western part of Organ Pipe and most of Cabeza Prieta and the Tinajas Altas region. Variety *coloradensis* is characterized by yellow or yellowish spines and spine sheaths, with the sheaths more inflated and the plants more robust and with a more upright growth habit than in var. *major*. Recent data collected by Baker suggests that var. coloradensis should be included within var. acanthocarpa.

Chollas in the flora called var. *major* are reported as primarily occurring in Arizona Upland areas including higher elevations in the flora area encompassing most of Organ Pipe and the eastern part of Cabeza Prieta. Variety *major* has been identified as having spines yellowish to commonly dark with dark and tightly fitting (not baggy) spine sheaths, and the plants generally being less robust and with branches more often spreading, and the joints shorter and not as densely spiny as var. *coloradensis*. These distinctions, however, are often feeble and plants identifiable as either variety can be found across the flora area, including plants next to each other. Another problem involves the neotype locality of var. *major* in Organ Pipe, which is confusingly situated in or near the zone of

reported intergradation; thus the epithet *major* has been used for the eastern populations more or less by convention (Felger & Zimmerman 2000).

According to Prof. Donald Pinkava (1999a), populations of *Cylindropuntia acanthocarpa* var. *thornberi* (Thornber & Bonker) Backeberg occur in northwestern Arizona. Variety *acanthocarpa* does not occur in the Sonoran Desert but var. *thornberi* does, just north of Phoenix at Table Mesa and in the Horseshoe Dam area. Marc Baker's research suggests that populations of var. *thornberi* are restricted to higher elevations east of those of var. *acanthocarpa* and north of those of var. *major*. In either case, the varieties *acanthocarpa* and *thornberi* are not entirely geographically or morphologically segregated. For example, Prof. Pinkava identified several specimens at ASU collected from the original type locality of *C. acanthocarpa* at Cactus Pass, Yavapai County as var. *thornberi* and specimens from the lectotype locality of *C. acanthocarpa* at Hillside, Yavapai County (see Benson 1982: 913) as approaching var. *thornberi*.

Since Benson (1969: 20) did not find the type specimen of *Opuntia echinocarpa* var. *major* Engelmann & J.M. Bigelow (*C. acanthocarpa* var. *major*) from the collection of Arthur Schott in 1855 (Engelmann & Bigelow 1856), he designated a neotype at the herbarium of Pomona College (POM) and reported a "Duplicate: Herbarium of the Organ Pipe Cactus National Monument." The neotype is indeed at the POM herbarium (incorporated into RSA) but no duplicate (it would be an isoneotype) was found at the Organ Pipe herbarium (ORPI) and it probably never was there. Steve Boyd at RSA (pers. comm. to Felger, 2005) wrote, "I feel like you were pretty lucky on this one. Benson's cacti were not well curated, with lots of things, including many he cited as neotypes, lacking determinations. I wouldn't be surprised if Benson never deposited the other specimen at Organ Pipe, based on what I've seen of his material, processed and unprocessed."

Cylindropuntia acanthocarpa might be confused with *C. echinocarpa*, and both are members of subgenus *Cylindropuntia*. In general *C. acanthocarpa* forms larger and more openly-branched plants and *C. echinocarpa* is more densely branched and more densely spiny with whiter spines, the plants are often smaller, and generally occur in drier, hotter areas, although their geographic ranges overlap. The fruit umbilicus (depression of flower scar on fruits) is usually shallow in *C. acanthocarpa*. "Seeds" (the seed enclosed in the bony aril) of the two species, at least among specimens from the flora area, are remarkably similar. In both species the developing seeds form facets or angles where they press against one another tightly packed in the developing fruit (the fruits lack a succulent matrix that might keep the developing seeds apart). Yet the seeds of *C. echinocarpa* are often somewhat smoother, with few angles or facets, and more nearly disk-shaped than those of *C. acanthocarpa*; and perhaps *C. echinocarpa* has fewer seeds per fruit than *C. acanthocarpa*. The differences, however, do not seem reliable enough to use as key characters. A difference in length of stem tubercles, however, is a reliable key feature that can be seen at any time of year. To add to the confusion, however, hybrids between the two species occur frequently in areas of sympatry. The putative hybrid, *C. ×deserta* (Griffiths) Pinkava, is morphologically intermediate and often bears flowers with intermediate coloration. Backcrossing may lead to the introduction of introgressant characters in otherwise typical individuals of either parent. Within the flora area there is a general trend for *C. echinocarpa* to more often occur in valleys and sandy soils, and *C. acanthocarpa* to be prominent on rocky slopes, even to peak elevations, and both can be common on bajadas.

Although the biological reality of the two varieties of *C. acanthocarpa* in southwestern Arizona can be problematic, they are reported to be distinguished as follows:

1. Plants branching at or near the base, branches mostly erect or ascending; sparsely branched; tubercles mostly greater than 6 mm wide and 6 mm high; spines ca. 18 per areole, the spine sheaths bright white or pale yellow, mostly absent after the first or second year; unsheathed spines dull yellow

or flesh colored or sometimes brown (on melanistic forms), sheathed central spines conspicuously wider (mostly more than 1 mm thick) and longer than auxiliary central spines and radials; contrast between the color of the new joints with sheathed spines and old joints with unsheathed spines is striking. ..... **Cylindropuntia acanthocarpa** var. **coloradensis**

1. Plants with a single stem or several stems from the base, erect or spreading, densely branched, tubercles mostly less than 5 mm wide and less than 6 mm high; spines ca. 12 per areole, the unsheathed spines bright pale yellow or whitish, brown, rust or grey and sometimes multi-colored; sheathed central spines not much thicker than 0.5 mm and not conspicuously wider than auxiliary central or radial spines. ..... **Cylindropuntia acanthocarpa** var. **major**

Figure 3. *Cylindropuntia acanthocarpa* var. *coloradensis*. (A & D) Kofa Queen Canyon, Kofa Mts, 5 Apr 2014. (D) note spine sheaths drop off after 1–2 years, revealing dull, beige-colored spines. (B & C) Near Horse Tanks, Castle Dome Mts, 6 Apr 2014. (B) note central spines distinctively larger than radial spines and sheaths whitish, reflective, and baggy.

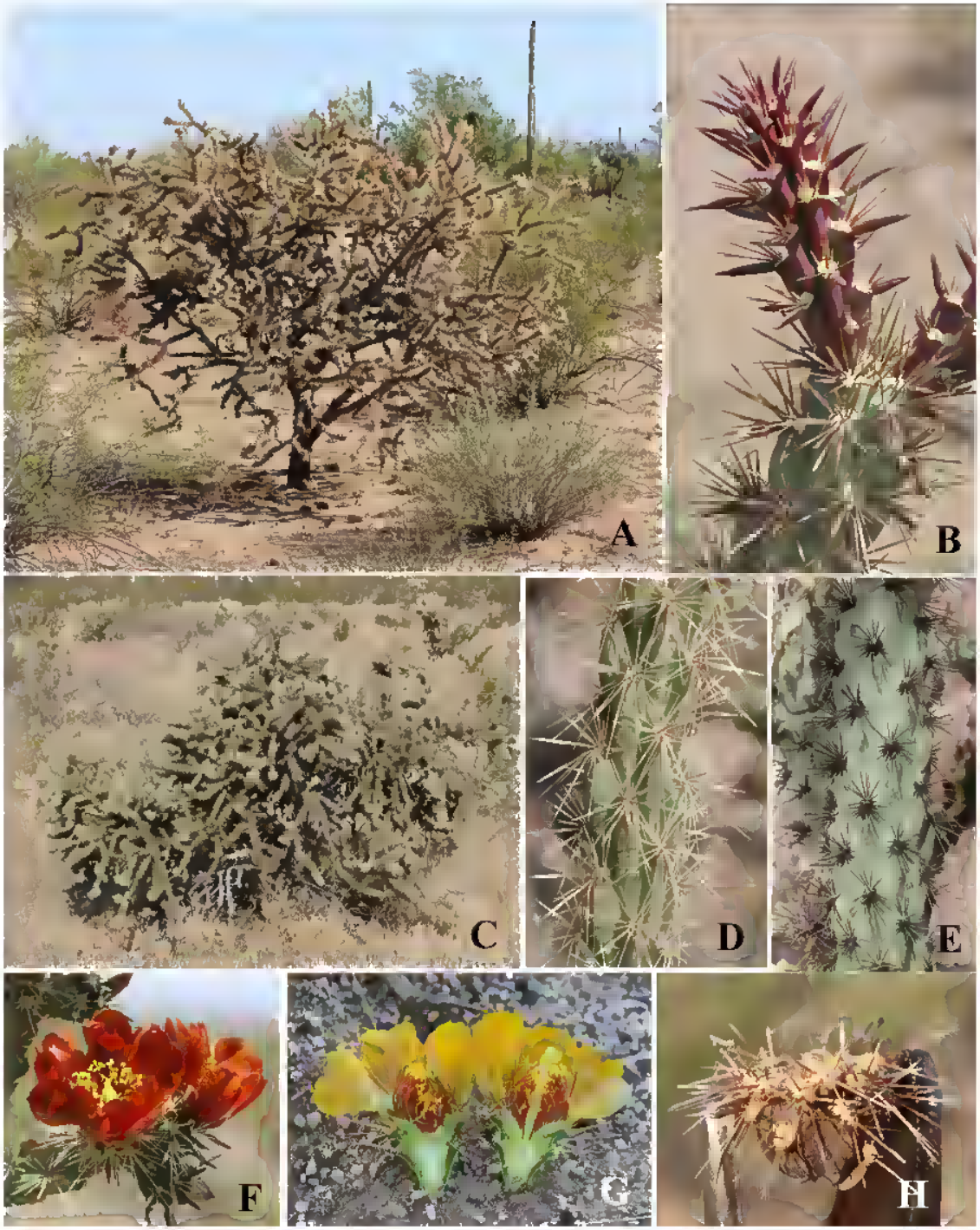

Figure 4. *Cylindropuntia acanthocarpa* var *major*. Valley of the Ajo, near intersection of Hwy 85 and Armenta Ranch Road. (A) 3 Jul 2013, (H) fresh, nearly dry fruit (held in tongs), 17 Jul 2013. (B) Developing stem with leaves, Ajo Mountain Drive, W of Ajo Mts, 2 Aug 2013 Alamo Wash, 1 mi E of Hwy 85 (C, D, E) 17 Jul 2013; (G) 23 May 2006. (F) Near N boundary of OP, E of Hwy 85, 12 May 2006

Cylindropuntia acanthocarpa var. **coloradensis** (L.D. Benson) Pinkava
[*Opuntia acanthocarpa* var. *coloradensis* L.D. Benson]. Figure 3.

OP: 1 km NNE of Red Tanks Well, 2000 ft, 4 Mar 1988, *Baker 7578* (ASU, ORPI 9771). 2 km NW of Dripping Springs, 525 m, 7 Mar 1988, *Baker 7587* (ASU, ORPI 8891). 0.8 km E of summit of Twin Peaks, 1740 ft, collected because of the odd flowering time, flowers brown-orange, 1 Aug 1990, *Baker 7883* (ORPI 9793). 2 km W of Hwy 85 at N boundary of Monument, [including] *C. leptocaulis, Ferocactus emoryi, Mammillaria grahamii, Opuntia engelmannii, O. fulgida var. fulgida, Peniocereus greggii*, 2 Dec 1990, *Felger 90-501* (both yellow-spined and dark-spined plants present). Granite hills, Gunsight Hills, E of Kuakatch, with *Larrea, Opuntia fulgida, O. leptocaulis, O. arbuscula, O. phaeacantha*, 14 Mar 2003, *Rutman 2003-533* (ORPI 14850). Mouth of Alamo Canyon, *Rutman 14 Apr 2003* (ORPI). Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger* (observation).

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 17004 & 17005* (SD). 3.1 mi W of intersection at Tule Well along Camino del Diablo, flowers golden-yellow with outer tepals showing some magenta, filaments red, anthers yellow, style cream, stigma cream-green, 5 Mar 1995, *Rebman 2883* (ASU, SD).

TA: E end of Tinajas Altas Pass, 12 Feb 1977, *Reeves R5395* (ASU). Mesa 1 km E of Tinajas Altas, 22 Nov 2008, *Felger 08-190*. Flats adjacent to granitic hills, SW side of Tinajas Altas range, 10 Jan 2002, *Felger* (observation).

Cylindropuntia acanthocarpa var. **major** (Engelmann & J.M. Bigelow) Pinkava
[*Opuntia echinocarpa* Engelmann var. *major* Engelmann & J.M. Bigelow, Proc. Amer. Acad. Arts 3: 305–306, 1856. *O. acanthocarpa* var. *major* (Engelmann & J.M. Bigelow) L.D. Benson]. Figure 4.

OP: Headquarters of the Organ Pipe Cactus National Monument, 2500 ft, sandy soil, 26 May 1962, *Steenbergh 5-2662-1* (neotype of *Opuntia echinocarpa* var. *major* Engelmann & J.M. Bigelow, POM 306088/RSA).

Variety not designated:

OP: Quitovaquito, 28 Nov 1939, *Harbison 26185 & 26192* (SD). Growler Well, *Nichol 27 Apr 1939* (ORPI 1154, det. Lyman Benson 1962). Aguajita Wash, 6 Apr 1988, *Felger 88-323*. 2.4 mi W of Hwy 85 on Puerto Blanco Drive, 19 Jun 1989, *Felger 89-225*. †Alamo Canyon, seeds, 1150 to 17,830 ybp (4 samples). †Montezuma's Head, seeds, 20,490 ybp. †Puerto Blanco Mts, on ridge, seeds, 980 to 9720 ybp (12 samples).

CP: Observations, *Felger*. Agua Dulce Pass, Eagle Tank, Buckhorn Tank, Cabeza Prieta Tanks, 13–15 Jun 1992; Childs Mt, 2845 ft, 18 Aug 1992.

TA: †Tinajas Altas, seeds, 1230 to 10,070 ybp (6 samples).

Cylindropuntia acanthocarpa × **C. spinosior**

There are two herbarium records for this putative hybrid in Organ Pipe. Sue Rutman found additional plants in the north-central part of Organ Pipe about two miles from the nearest known *C. spinosior*. Fruits of the hybrid are yellow, spiny, and dry earlier than those of *C. spinosior* but later than those of *C. acanthocarpa*. *Cylindropuntia acanthocarpa* has dry, spiny fruits and *C. spinosior* has fleshy yellow, and spineless fruits.

OP: W of Bates Mts, plants to 2 m tall, with *Opuntia arbuscula, O. leptocaulis, O. fulgida*, etc., 23 Mar 1990, *Baker 7774* (ASU). Just across international border from Las Palmas, 1410 ft, just S of Dos Lomitas, UTM 12 334300 3526300, *Atriplex polycarpa* flats with *Larrea, Opuntia fulgida, O. leptocaulis, Peniocereus greggii, Prosopis glandulosa*, shrub 1.8 m tall, flowers red-purple, style pale red-purple above, pale green-yellow below, stigma cream-white, fruits pale green and/or yellow, often tinged with red-purple, especially about areoles, 23 May 1991, *Baker 8366* (ASU, SD).

Cylindropuntia arbuscula (Engelmann) F.M. Knuth
[*Opuntia arbuscula* Engelmann]
Pencil cholla; *siviri, tasajo*, vipinoi. Figure 5.

Shrubby chollas, 0.8–2+ m tall, sometimes with a thick woody trunk, much branched above, with a dense crown. Smaller (ultimate) joints readily detaching, mostly (3.5) 4–15 cm × (7) 8.5–12 mm, green to yellow-green all year, tubercles scarcely raised; areoles rather widely spaced; spines 1.8–3.5 cm long, slender, mostly one spine per areole, less often 2 or 3, the lower areoles on each joint mostly spineless. Flowers 2–3.5 cm wide, inner tepals greenish yellow, yellow, or yellow-brown, outer tepals reddish, purple, or orange, filaments green, anthers yellow. Fruits fleshy, often produced in large quantities and 1 or often several fruits at a stem tip, often persistent for about 1 year, 2.3–2.8 cm × 10.7–12 mm, sometimes enlarging with age, yellow-green or green even when ripe, or sometimes with slight reddish or yellowish tinge, the umbilicus (the top the fruit) unusually deep. Flowering April and early May. $2n = 66$.

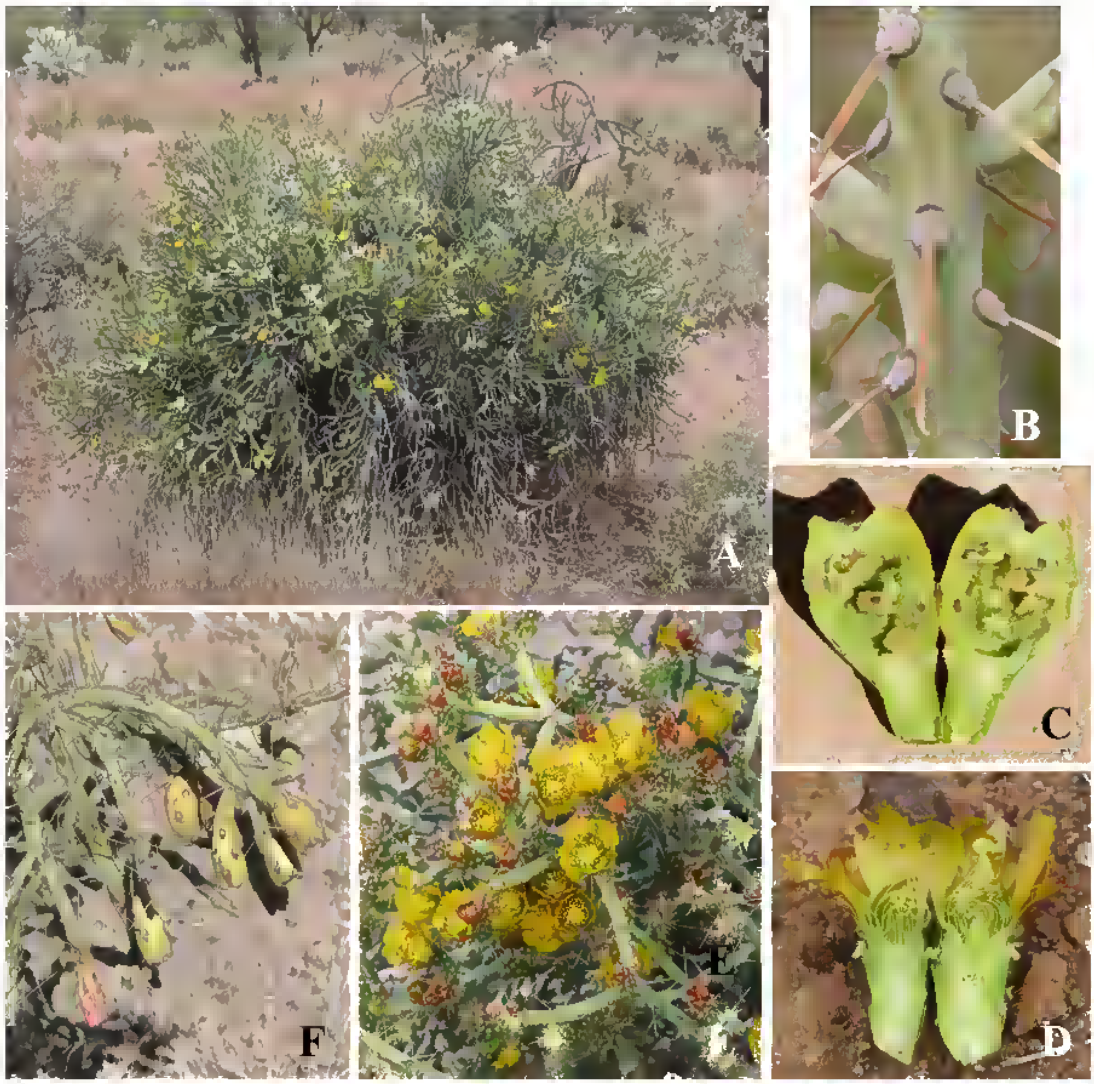

Figure 5. *Cylindropuntia arbuscula*. (A, D, & E) Ajo, 30 Apr 2005. Sandy plain near Kuakatch Wash west of Hwy 85. (B) portion of stem, 4 Mar 2009; (C) fruit, 28 Feb 2008. (F) Redondo Valley, N of Why, 20 Jan 2008.

Widely scattered in Organ Pipe, mostly in sandy loam soils of valley bottoms and bajada plains, and sometimes along the margins of arroyos. Also at the eastern extent of Cabeza Prieta between the Growler Mountains and Daniel's Arroyo, where this cholla thrives in narrow gullies cut into caliche terraces. This cholla does not range farther westward from the flora area.

Arizona from Maricopa County southward and Sonora southward to the coastal plain southeast of Guaymas.

Cylindropuntia arbuscula is hexaploid, $2n = 66$ (e.g., Pinkava 2003a). Pentaploid chollas, which often form local clones, have been called *C. arbuscula* (Pinkava 1999a) but are probably hybrids with *C. arbuscula* as a parent or are hybrids with a different origin than *C. arbuscula* (*C. arbuscula* is likely of hybrid origin with *C. leptocaulis* as one of its parents). Marc Baker determined chromosome numbers of *C. arbuscula* from various locations in Pima County and elsewhere and concludes that most individuals of true *C. arbuscula* ($2n = 66$) generally bear only a single spine per areole on mature stems and sporadically two or three spines per areole. The pentaploids, which include the clonal microspecies *C.* ×*neoarbuscula* F.M. Kunth and *C.* ×*vivipara* F.M. Kunth and probably a few other unnamed clones of hybrid origin, all generally bear three or more spines per areole on mature stems.

Gila River Pimas cooked the buds and fruit in the same manner as those of *C. acanthocarpa*, but *C. arbuscula* fruits were said to taste different, being a bit more sour (tart) than those of *C. acanthocarpa*. Pencil cholla buds and fruits were often dried for future use (Rea 1997). O'odham plant expert, Juanita Ahil (1915–1994) preferred pencil cholla buds and fruits when she could find them, rather than those of other chollas (Martha Ames Burgess, pers. comm. to Felger, 2014). The fleshy fruits are eaten fresh by the Seris (Felger & Moser 1985).

OP. Senita Basin, 23 Mar 1969, *Lehto 15428* (ASC). Growler Canyon, 1400 ft, 19 Oct 1987, *Baker 7573* (ASU, ORPI 8887). 1 mi W of Hwy 85 on Kuakatch Wash Road, 24 Jul 1978, *Bowers 1381* (ORPI 1982). Rocky slope 0.5 km N of Aguajita Spring, 6 Apr 1988, *Felger 88-321*. Hocker Well, 3 Dec 1990, *Felger* (observation).

CP. 2 km SW of Cameron's Tank, 1650 ft, UTM (Zone 12N) 317400 E, 3568250 N (NAD 1927), *Malusa* (observation), 8 Feb 2000.

Cylindropuntia bigelovii (Engelmann) F.M. Knuth
[*Opuntia bigelovii* Engelmann]
Teddybear cholla, jumping cholla; *choya gïiera*; hadsadkam (also called hanamï, the general term for cholla). Figure 6.

Chollas often 0.5–1.8 (2) m tall, the trunk erect, stout, straight, and beset with dead, persistent branches (joints) with blackened spines. As with many chollas, the root system is a cluster of fibrous roots with a few horizontal lateral roots of indeterminate lengths. Joints relatively short and thick, and readily detaching, green all year, with extrafloral nectaries (areolar glands) green when fresh, seen on the new growth. Spines dull yellow and densely covering and obscuring the stems segments (joints), and with prominent yellowish spine sheaths. Flowers yellow-green, 3.5–5.5 cm wide, attached more firmly than the ultimate joints. Inner tepals 8–10, widely separated and not completely ringing the receptacle and not hiding the short outer tepals; inner tepals 2.5–3 × 1 cm, pale yellow-green, the margins essentially colorless and erose. Filaments bright green; anthers bright yellow, often stunted and lacking pollen. Flowering March and April. Fruits mostly 3–3.5 × 2–2.5 cm, yellow, solitary, leathery and moderately fleshy, strongly tuberculate, spineless or with slender bristle-like deciduous spines 9–15 mm long, becoming spineless or essentially so at maturity; fruits might persist for many months under favorable conditions, or soon falling away during drier conditions. Seeds variously present or absent.

Abundant and widespread on desert pavements, sandy plains and flats, bajadas, pediments, and rocky slopes of the hotter, drier mountains, and to at least 2725 feet in the Ajo Mountains and to 3150 feet in the Gila Mountains near the Tinajas Altas Mountains. It has been in the flora area for at least 15,700 years.

Southeastern California, southern Nevada, southern and western Arizona, eastern Baja California, northeastern Baja California Sur, and northwestern Sonora

Figure 6. *Cylindropuntia bigelovii*. (A) Gunsight Hills, 15 Apr 2012. Organ Pipe headquarters. (B & C) 18 May 2006, (D & E) 23 May 2010. (F) Bates Well Road, W of Bates Well, 20 Mar 2005.

This cholla is primarily a clonal species. The upper or younger joints fall at a touch, and the spines are difficult and painful to pull out of your flesh. The plants propagate prolifically from readily-rooting fallen joints. The resulting mine-field of spines is a serious hazard to the walker. This most feared plant of the flora area is nonetheless lovely when the dense cover of spines catch the early- or late-day sun, creating a golden halo. Yet you need only one encounter with this fierce cholla to forever change your behavior: never again will you take a step back without first looking behind you. In southern Arizona this cactus is often called jumping cholla. Here's why: you could easily pick up a joint of *C. bigelovii* on, say, your *left* boot while walking, un-noticed until your natural gait deposited the joint onto the back of your *right* leg (calf or pants, depending), about a foot off the ground. Hence the name jumping cholla–how else did it get up there? Hornaday (1908: 221) called it, "Bigelow's Accursed Cholla" and said, "The worst thing about that Cholla is its treachery." Half a century earlier, Bigelow (1856: 13) himself wrote, "We find (February 7) a new species of *Opuntia* (described by Engelmann as *O. bigelovii*), with a reticulated woody stem, very fragile at the joints before hardening into wood, and armed with spines worse than those of a porcupine. It is called by the Mexicans, 'chug.' The plant is the horror of man and beast. Our mules are as fearful of it as ourselves. The barbed spines stick so fast in the flesh that the joint of the plant is separated from the main stem before the spines can be withdrawn." They were somewhere between the area of Wikieup (Mohave County, Arizona) and what is now the Alamo Lake area (La Paz County).

All plants sampled at Organ Pipe Monument (by Marc Baker) are triploid (Pinkava et al. 1992a); consequently there is very little chance of the seeds being viable. Pollen production is highly variable in this species; at least the triploid plants produce relatively few pollen grains. In the Tucson region pollen production may be higher in seasons of high rainfall and lower during drier periods (Mary Kay O'Rourke, in Felger & Zimmerman 2000). In addition, populations of *C. bigelovii* within the Tucson area appear to be primarily diploid (Baker et al. 2009). It has been suggested that the success of triploid apogamy, which is a common occurrence in *C. bigelovii*, *C. fulgida*, and *C. leptocaulis*, lies in its ability to fix and maintain particularly adaptive genomes (Baker & Pinkava 1987). *Cylindropuntia bigelovii* and *C. fulgida* have fewer inner tepals than most other chollas. Reduction in the perianth correlates with asexual reproduction, as might be expected with reduced selection pressure by pollinators. *Cylindropuntia bigelovii* has thicker, generally shorter, and more densely spiny joints and extends into more arid regions than does *C. fulgida*.

The Cahuillas pit-baked the buds (Bean & Saubel 1972) and Seris pit-baked young stem segments and made a diuretic tea from the roots (Felger & Moser 1985). O'odham and Seri graves were often covered with brush and chollas, often this species, to discourage animals such as coyotes from digging (Felger & Moser 1985; Rea 1997). Gila River Pimas used pieces of this cholla as barricades against marauding animals in their fields (Rea 1997).

OP: 1.8 km NW of Red Tank Well, 5 Mar 1988, *Baker 7582* (ASU, ORPI). 2 km NW of Dripping Springs, 7 Mar 1988, *Baker 7588* (ASU, ORPI). W slopes of Diablo Mts, 2 Dec 1990, *Felger* (observation). †Puerto Blanco Mts, on ridge, seeds, 980 to 10,500 ybp (7 samples)

CP: Agua Dulce Mts, 1200 ft, 14 Apr 1941, *Benson 10766*. Cholla Pass, 3 8 km ESE of Sheep Mtn, 325 m, 5 Jul 2000, *Baker 13839* (ASU, SD). Cholla Pass, 11 Apr 1978, *Lehto L22500* (ASU). Observations, *Felger*. Eagle Tank, 13 Jun 1992, Childs Mt, 2845 ft, 18 Aug 1992.

TA: Tinajas Altas, 14 Feb 1894, *Mearns 348* (US). 0.5 km N of Tinajas Altas, 12 Feb 1977, *Reeves 5393* (ASU). Flats at SW side of Tinajas Altas range, 10 Jan 2002, *Felger* (observation). †Tinajas Altas, seeds, 1230 to 15,680 ybp (10 samples). †Butler Mts, spines, seeds, 11,060 ybp.

Cylindropuntia echinocarpa (Engelmann & J.M. Bigelow) F.M. Knuth
[*Opuntia echinocarpa* Engelmann & J.M. Bigelow. *O. wigginsii* L.D. Benson]
Silver cholla. Figure 7.

Small chollas, often 20–75 (100) cm tall, and usually shorter in the driest, western areas where the plants are often dwarfed. Primary stem(s) of larger plants mostly erect, or sometimes stiffly horizontal just above the soil surface. Joints (1.5) 5–13 × 1.8–3.2 cm, firmly attached or smaller ones sometimes readily detaching; stem tubercles 12–16 mm long, usually less than twice as long as broad. All areoles densely spiny; spines whitish to yellow and densely covering and obscuring the stem segments; spine sheaths yellowish or whitish (silvery). Flowers 1–4 from a single joint; often 5.5–6.5 cm wide. Inner tepals about 2 cm long, shiny pale greenish yellow to silvery white. Filaments green to greenish yellow (not brilliant green as in *C. bigelovii*); anthers yellow. Flowering March and April. Fruits often 15–20 × 17–22 mm, dry upon ripening in late May and early June, bur-like with bristly spines, and not persistent. $2n = 22$.

Widespread and common across the Tinajas Altas region and the western part of Cabeza Prieta; sandy flats, dunes, creosotebush flats, hills, and mountain slopes. This cholla does not range eastward from Cabeza Prieta in the flora area, but does occur to the northeast in Maricopa County.

Western Arizona, northwestern Sonora, northeastern Baja California, southeastern California, southern Nevada, and southwestern Utah.

The flower buds and young cladodes were prepared in a similar manner as those of *C. acanthocarpa* and often constituted a staple food in spring (Castetter & Bell 1942; Castetter & Underhill 1935).

This species commonly hybridizes with *C. acanthocarpa*, as discussed under that species, to a much lesser extent with *C. leptocaulis* (e.g., *C. echinocarpa* × *C. leptocaulis*, Lechuguilla Desert north of Wellton Hills, Yuma Co., 10 Jan 1994, *Baker 11275* (ASU), and very rarely with *C. ramosissima* (the first documented specimen of *C. echinocarpa* × *C. ramosissima* is from Clark Co., NV, 20 Apr 2012, *Baker 18102*, specimen to be deposited at ASU).

CP: T13S, R14W, S24, 6 Apr 1979, *Lehto L23485* (ASU) 0.8 mi SE of Tule Well on Camino del Diablo, 16 Jun 1992, *Felger 92-623*. 24.5 mi SW of boundary with Organ Pipe en route to Pinta Sands, 4 Mar 1995, *Rebman 2881* (ASU, DES, SD). Observations, *Felger* Christmas Pass, 14 Jun 1992, Pinta Sands, 1 Feb 1992.

TA: SE side of Tinajas Altas Mts, 32°18'N, 114°02'W, 3 Feb 1990, *Felger* (observation).

Cylindropuntia fulgida (Engelmann) F.M. Knuth
[*Opuntia fulgida* Engelmann]
Chain-fruit cholla, jumping cholla; *choya*; hanamī

In southern Arizona this cactus is generally called chain-fruit cholla, and the name jumping cholla generally is reserved for *C. bigelovii*.

This species ranges from southern Arizona to northwestern Sinaloa. (The single specimen from southwestern New Mexico [*Bird 3341*, UNM] is of questionable provenience and identification, or possibly adventive [Allred & Ivey 2012].) Variety *fulgida* apparently does not extend south of the Guaymas region in Sonora. Seeds resembling *C. fulgida* (little wedges crammed together) have been found in the Puerto Blanco Mountains dating to 3400 years old. Although in most cases the varieties are readily distinguished, *C. fulgida* var. *mamillata* probably does not deserve taxonomic recognition, as it is merely a form interspersed among the typical forms, except that the *mamillata* form becomes dominant toward the southern part of the geographic range of the species. *Cylindropuntia fulgida* is replaced in the Baja California Peninsula by the closely related and similar-appearing *C. cholla* (F.A.C. Weber) F.M. Knuth.

OP: †*C.* cf. *fulgida*, Puerto Blanco Mts, on ridge, seeds, modern (30) to 3400 ybp (6 samples).

Figure 7. *Cylindropuntia echinocarpa*. (A & C) Dunes 20 mi S of Sonoyta on Hwy 8, Sonora, 27 Mar 2010. (B) W side of Gila Mts, 16 Mar 2013, photo by Jim Malusa.

1. Spines dense, interlaced, and obscuring the stem surface, with loose-fitting papery sheaths, the larger spines usually 2.5–3.5 cm long……..... **Cylindropuntia fulgida** var. **fulgida**
1. Spines relatively sparse, not interlaced, and not obscuring the stem surface, with tight-fitting (not papery) sheaths, the larger spines 1–2 cm long…..... **Cylindropuntia fulgida** var. **mamillata**

Cylindropuntia fulgida var. **fulgida**
[*Opuntia fulgida* var. *fulgida*]. Figure 8.

Shrubby to arborescent chollas, often 1–2.5 (rarely to 4+) m tall; trunk well developed, reaching 25 cm diameter, and often with several major branches, and a broad, much-branched crown. (Some are tall enough that you can stand in the shade of a spreading cholla, being mindful of spiny joints overhead and fallen joints littering the ground.) Smaller branches and joints, mostly at the crown or top of the plants, the joints green all year, detaching at the slightest touch, earning the name "jumping cholla." The joints densely spiny, the spines usually obscuring the stem surface; spine sheaths large, golden yellow to straw colored; tubercles longer than wide and prominent; stem tissue often becoming blackish or gray on drying (nearly all herbarium specimens of *C. fulgida*, as well as the closely related *C. cholla*, are blackish or gray; also see *Carnegiea* and *Lophocereus*).

In Organ Pipe flowering primarily starts before the summer rains and continues into July, although flowering is documented in the region from late April through August. Flowers 2.5–5 cm wide. Inner tepals bright pink-purple, spreading widely and sometimes curling back, relatively few and not totally ringing the flower, the larger tepals often 14–20 × 6–7 mm. The tepals, stamens, and style usually fall as a unit. Filaments bright purplish pink, or the inner filaments sometimes white; anthers white. Stigma white. The flowers open in the late afternoon, sometimes not until 6 pm, remain open during the night, and wither before dawn, or they may also open in the early morning. Flowers visited by medium-sized moths at night and by medium-sized bees during daylight. Fruits green and fleshy, often 3–6 × 2–4.8 cm, mostly obovoid, remaining green and fleshy, usually persisting for at least several years and proliferating in hanging chains of (3) 6–18 fruits, the longer chains often swaying in the wind.

Widespread and often abundant, mostly in lowlands on bajadas, desert flats and along margins of large washes, and less common on rocky slopes and alkaline flats, and up to about 2775 feet in the Ajo Mountains; Organ Pipe and Cabeza Prieta westward to the vicinity of Tule Well. Bighorn sheep and Sonoran pronghorn relish the fruits and may depend on them for water (moisture) during extreme drought. This cholla is essentially at its western geographic range in Cabeza Prieta.

Propagation is vegetative from readily-rooting fallen joints and fruits (Toumey 1845). *Cylindropuntia fulgida* is mostly diploid, but triploid individuals are common. Diploid individuals of *C. fulgida* exhibit lower pollen fertility than do most other non-apomictic cholla species and triploid individuals exhibit even lower pollen fertility (Baker & Pinkava 1987). Although reproduction by seed has not been observed in the flora area it probably occurs to some extent. For a summary discussion of the life history of this species see Turner et al. (1995).

The fleshy fruits are available all year and were often a significant food resource for local people. The fruits were consumed fresh or cooked and could be dried and stored (Castetter & Bell 1942; Castetter & Underhill 1935; Felger & Moser 1985; Nabhan et al. 1982). Dried, black gum that accumulates on the stem from injuries is edible and has been much appreciated by Seris and Yaquis (Felger 2007; Felger & Moser 1985). This dried gum is ground, cleaned, and cooked, often in animal fat, or eaten uncooked with water added. The stems, gum, fruits, and roots also have been used medicinally (Felger 2007; Felger & Moser 1985).

OP: Bates Well, 20 Nov 1939, *Harbison 26170*; 13 mi S of Rocky Point Junction [Why], 19 Aug 1961, *Tschirley T-80*; Vicinity of Aguajita, 29 Mar 1988, *Felger 88-130*; Estes Canyon picnic area, 16 May 1989, *Baker 7753* (ASU); Observations, *Felger*, Hwy 85 at N boundary of Monument, 23 May 1991, Hocker Well, 3 m tall, chains of 9–18 fruits, 3 Dec 1990.

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 17059* (SD); Cholla Pass, 11 Apr 1978, *Lehto L-22499* (ASU); 5 mi E of intersection at Tule Well along Camino del Diablo, 5 Mar 1995, *Rebman 2888* (ASU, DES); Observations, *Felger*, Bajada and on N side of Agua Dulce Mts, 31 Jan 1992, 6 mi eastward from Tule Well on Camino del Diablo, 28 Nov 2001.

Figure 8. *Cylindropuntia fulgida* var. *fulgida*. (A & B) Hwy 85 at mile marker 68 [10 highway mi S of N boundary of OP], 7 Jun 2006. (C) Chain of fruits, trail to Victoria Mine, Puerto Blanco Mts, 28 Feb 2009. (D) Between Hwy 85 and Armenta Ranch, 30 Jul 2013. (E) Coffeepot Well, BLM land, 28 Apr 2006.

Cylindropuntia fulgida var. **mamillata** (Schott ex Engelmann) Backeberg
[*Opuntia fulgida* Engelmann var. *mamillata* (Schott ex Engelmann) J.M. Coulter]. Figure 9.

Rare in the northeastern part of Organ Pipe where it occurs as single plants or groups of less than about 10 plants. In this region plants of var. *mamillata* are shorter than those of var. *fulgida*. Variety *mamillata* is more common immediately eastward and northward from the Monument border. A nearby population extends for several miles west of Quijotoa near Arizona Hwy 86 and there is a very large population near Coffee Pot Mountain in the Sauceda Mountains in the Goldwater Range.

OP: Near Kuakatch, 2 m tall, 10 Apr 2000, *Rutman* (photo). Hwy 85 near milepost 67 (near N boundary), one plant, 27 May 2001, *Rutman* (photo).

Figure 9. *Cylindropuntia fulgida* var. *mamillata*. Near Coffeepot Mtn, 28 Apr 2006.

Cylindropuntia leptocaulis (de Candolle) F.M. Knuth
[*Opuntia leptocaulis* de Candolle]
Desert Christmas cholla; *tasajillo*, 'ajĭ vipinoi, ce'ecem vipinoi. Figure 10.

Slender-stem chollas, 0.5–1 m (reaching 1.5+ m when growing through shrubs). Young plants with a single, somewhat tuberous root. Mature plants somewhat shrubby or often strict, with main branches long, straight, erect to sub-erect, and arising from near plant base. Young stems (joints) 4.8–6.6 mm diameter (sometimes shriveling to 3 mm in drought), green all year, the surfaces relatively smooth with low, poorly defined tubercles. Areoles spineless or producing a single spine often 1.5–8 cm long with a deciduous yellowish sheath. Larger and longer branches often bearing many and much smaller "short shoots" (joints), these mostly at right angles to the main axes, readily detaching, and often bearing glochids but no spines.

Flowers 1.5–2 cm wide, usually opening late in the afternoon or near dusk and remaining open in the early evening (in late May observed opening at 4 p.m. and closing at 7:30 p.m.). Inner tepals about 1 cm long, pale yellow-green to cream-white, outer tepals red-purple. Stamens very sensitive, rapidly converging when touched. Filaments, anthers, style, and stigma cream colored. Flowering April and May and after summer rains. Fruits mostly ripening November and December, and often persisting at least until May, or some fruits retained all year. Fruits (10) 14–22 × 8 mm, broadly ellipsoid to obovoid, fleshy, the skin red, the pulp pale yellow-orange, with widely separated areoles bearing tufts of small glochids, often also with larger fruits 25–30 × 8.5–10.5 mm, obovoid to clavate, both classes of fruits several-seeded or sometimes seedless, and sometimes producing a short

green joint or a second fruit from 1 or more of the upper areoles. Seeds 4.3–4.5 mm diameter. The small, fleshy fruits, red when ripe, can be eaten fresh, after removing the glochids (Chico Suni in Felger et al. 1992, Rea 1997).

This species is notable for its slender stems and small, fleshy, red fruits often on "short shoots" along the length of the longer, terminal stems. It is not very formidable in appearance, but when tucked into a runnel among creosotebush and bursage, it is painfully easy to blunder into a spiny Christmas cholla.

Figure 10. *Cylindropuntia leptocaulis*. (A, C, & E) Bajada W of Sikort Chuapo Mts, 4 Mar 2009. Hwy 85 near N boundary of Organ Pipe. (B & D) 22 May 2006, (F) 21 Mar 2010

Widespread in many habitats in Organ Pipe and Cabeza Prieta including sandy to gravelly, silty or rocky soils of washes, canyons, bajadas, creosotebush flats, and slopes; often growing in association of shrubs and desert trees. The series of years prior to about 2010 with below-average rainfall caused a widespread die-off of this cactus throughout the flora area. It was in the Puerto Blanco Mountains about 1000 years ago. There are two chromosome races in the flora area, diploid and triploid, which are morphologically indistinguishable and occur intermixed (Baker et al. 2009).

Arizona to Oklahoma and Texas, and Mexico southward to northwestern Sinaloa and Puebla. This is the most slender-stemmed of the chollas and the most wide-ranging geographically. Despite geographical and cytological variation, it does not seem practical to recognize infraspecific taxa, although Bravo-Hollis (1978) lists eight varieties. Reports of *Cylindropuntia leptocaulis* from the Baja California Peninsula refer instead to the closely related *C. lindsayi* (Rebman) Rebman. Although this species hybridizes with several others, only hybrids with *C. echinocarpa* have been recorded from vicinity of the flora area (see *C. echinocarpa*).

OP: Cipriano Well, *Nichol 27 Apr 1939* (ORPI). ¼ mi N of Kuakatch Wash Road on power line road, 24 Jul 1978, *Bowers 1383* (ORPI). 0.9 mi W of Quitobaquito, 14 Sep 1988, *Felger 88-470*. Observations, *Felger* Dos Lomitas, 23 May 1991; Hocker Well, very common, 3 Dec 1990. †Puerto Blanco Mts, on ridge, stems, 30 & 990 ybp (it presently grows in the nearby canyon bottom and not on the slopes or ridge).

CP: Tule Wells, 11 Mar 1937, *Harbison 16832* (SD). Observations, *Felger*. Agua Dulce Mts, 31 Jan 1992; Namer's Grave, 1 Feb 1992; 3 km WNW of Little Tule Well, Packrat Hill, near Dos Playas, and Mohawk Valley, 12 & 13 Jun 1992. 3.1 mi W of the intersection at Tule Well along the Camino del Diablo, 5 Mar 1995, *Rebman 2886* (ASU, DES, SD).

††**Cylindropuntia multigeniculata** (Clokey) Backeberg

This low shrub cholla grew in the Ajo and Puerto Blanco Mountains at least 9600 to 32,000 years ago in *Yucca brevifolia–Juniperus californica* woodland that may have been similar to the present day habitat for *Cylindropuntia multigeniculata,* which occurs in Mohave County, Arizona, and Clark County, Nevada. The fossil material was originally thought to be of *C. whipplei* (Engelmann & J.M. Bigelow) F.M. Knuth (Felger et al. 2013b; Van Devender 1987, 1990), but was identified as *C. multigeniculata* by Marc Baker in 2013. See Baker and Cloud-Hughes (2014) for identification and description of *C. multigeniculata* and relationships with other spiny-fruited chollas.

OP: †Alamo Canyon, seeds, 9570 to 32,000 ybp (4 samples). Montezuma's Head, 13,500 to 21,840 ybp (4 samples.) †Puerto Blanco Mts, on ridge, stems, seeds, 14,120 ybp

Cylindropuntia ramosissima (Engelmann) F.M. Knuth
[*Opuntia ramosissima* Engelmann]
Diamond cholla. Figure 11.

In California this cactus is often called pencil cholla (Pinkava 2003a), a name reserved for *C. arbuscula* in Arizona. Slender-stem chollas often 0.3–0.8 (1.2) m tall, usually broader than tall, sometimes with short, thick, woody trunks, the principal branches mostly basal; sometimes forming spreading colonies. (Individuals of this species, if left unmolested, generally form a single-trunked shrub but the substrate underneath the plants are often a preferred site for the nesting of rodents. The rodent activities can cause the plant to topple and produce new roots where its younger stems touch the soil.) Stem segments (joints) firmly attached, 6.5–9 mm diameter, dull greenish to gray-green. Spines on some joints sometimes none, or 1 per areole in upper portion of each joint, (1.5) 2–8.5 cm long, with deciduous straw-colored sheaths. Areoles linear, recessed, each forming a conspicuous longitudinal groove in the upper end of its subtending tubercle, the glochids mostly buried in the groove; young stem and floral areoles with small, dense tufts of white hairs. Tubercles very low but sharply defined, their outlines diamond-shaped (hence the common name).

Figure 11. *Cylindropuntia ramosissima*. (A) S of San Cristobal Wash, N of Camino del Diablo, 27 Dec 2013. (B) Crater Range, near Hwy 85, 31 Jan 2009. Collected 18 km NNE of Amboy, San Bernardino Co., CA and relocated to Prescott, AZ, *Baker 17047 1*. (C) 27 Jul 2010; (E) near ripe fruits, 7 Sep 2010; photos by Marc Baker. (D) Anza Borrego Desert State Park, photo by Bill Sullivan for ABD Natural History Assoc.; (F) East of San Cristobal Wash and north of Camino del Diablo, 23 Nov 2013.

Flowers 2.5–3 cm wide. Inner tepals pale yellow-brown to cream-color, some suffused medially near apex with red-purple. Filaments bright green, the anthers bright yellow. Style and stigma cream colored. Flowering late April and early May and often after summer rains; flowers opening in mid- to late afternoon, often about 3 p.m. and closing 1–2 hours after sunset. Developing

fruits with accrescent spines; mature fruits characteristically dry, 17.5–42 × (6.5) 8.3–10.7 mm, mostly persistent, densely spiny, the longer spines 14–22 mm. Fruits ripening late May and June or after summer rains. During the exceptionally wet El Niño year of 1991–1992, ripe, fleshy fruits persisted until late January and early February.

Common in scattered localities across the lowlands of Cabeza Prieta and Tinajas Altas, mostly on well-drained soils of valley plains, flats, and bajadas, and sometimes on low hills. Especially common along the western side of the Lechuguilla Valley in the Goldwater Range and the Tinajas Altas region. Also two records at the western margin of Organ Pipe where it grows in sandy soil. Both diploid and tetraploid races of *C. ramosissima* occur in the flora area. No morphological characteristics have been found to distinguish the two races, although tetraploid individuals tend to occur on sandy substrates and diploid individuals tend to occur on rocky substrates (Baker et al. 2009). Diamond cholla at the latitude of the flora area halts its eastern march along the western reaches of Organ Pipe, although it does range farther eastward in central Arizona. It has been in the Tinajas Altas region for more than 10,000 years.

There was also widespread and significant die-off of *Cylindropuntia ramosissima* from the north end of the Growler Mountains through the San Cristobal Valley, with greater than 90% mortality in the valley, but less towards the Growler Mountains. In March 2014, Rutman found a clonal colony about 10 m wide, due to root crown spreading, near the northern tip of the Growler Mountains in the Goldwater Range. It was located on a lower bajada with a Pleistocene surface with *Ambrosia deltoidea*, *A. dumosa*, *Krameria bicolor*, and *Larrea*.

Western Arizona, southeastern California, southern Nevada, southwestern Utah, northwestern Sonora, and Baja California.

Bean and Saubel (1972) report that the fruits were eaten fresh or dried for later use. The stems, with the spines removed, were boiled into a soup or dried for future use. However, the fruits very quickly become dry on maturing and hardly seem edible when fresh—there obviously is a lot we don't know about the intricate relationships of people and plants in our deserts.

OP. W of Bates Mts, sandy flat, 23 Mar 1990, *Baker 7776* (ASU, ORPI)

CP. 7 mi E of Papago Well, *Harbison 15 Nov 1937* (SD). Lower Well, *Simmons 17 May 1963* (CAB). San Cristobal Wash on road to Papago Well, 31 Jan 1992, *Felger 92-3*. 2 mi on Charlie Bell Road WNW of Little Tule Well, 12 Jun 1992, *Felger 92-539*. Cabeza Prieta Mts, 14 Jun 1992, *Felger* (observation). Growler Valley, 1.4 mi W of W boundary of OP on Camino del Diablo/Bates Well Road, *Rutman 28 Sep 2013*.

TA. E end of Tinajas Altas Pass, 12 Feb 1977, *Reeves 5394* (ASU). SW side of Tinajas Altas range, flats adjacent to granitic hills, 10 Jan 2002, *Felger* (observation). Camino del Diablo SE of Raven Butte, 25 Oct 2004, *Felger 04-08*. †Butler Mts, stem, 10,360 ybp.

Cylindropuntia spinosior (Engelmann) F.M. Knuth
[*Opuntia spinosior* (Engelmann) Toumey]
Cane cholla. Figure 12.

Shrubby chollas to 1.8 m tall, the trunk erect or nearly so. Stems become purplish in winter and dry seasons. Joints 5–20 cm long and moderately thick, firmly attached, and often arranged in whorls. Flowers April and May, showy; inner tepals rose-purple, 1.8–3.5 cm long. Filaments rose-purple; anthers white. Fruits fleshy, yellow, knobby, spineless, and semi-persistent.

Widely scattered and rather rare on *Larrea* flats in Organ Pipe and the eastern margin of Cabeza Prieta in the vicinity of Adobe Well where it is locally common. It grows on clay loams on lower bajadas and upper valley floors, where this species is at its westernmost limit in southern

Arizona. However, it ranges farther west in northern Arizona. Perhaps the 1939 record from Quitobaquito is from a transplanted cholla because it has not been documented there since. Hybridization with *C. acanthocarpa* and *C. versicolor* is discussed under those species.

Figure 12. *Cylindropuntia spinosior*. (A) Why, 5 May 2005. Hwy 86 west of Quijotoa, Pima Co. (B) 18 May 2006, (C & D) 1 May 2005, (F) 8 May 2006. (E) Hwy 85 near Why, 6 Nov 2013.

Widespread in Arizona, especially at and above the upper elevation limits of the desert. Also New Mexico, northern Sonora, and Chihuahua. The fleshy fruits are edible.

OP. Quitobaquito, 28 Nov 1939, *Harbison 26188* (ARIZ, SD). Growler Canyon, 19 Oct 1987, *Baker 7572* (ASU, ORPI).

CP. 0.8 km E of Adobe Well, 12 Jun 1992, *Felger 92-546* (ARIZ, AU).

Cylindropuntia versicolor (Engelmann ex J.M. Coulter) F.M. Knuth
[*Opuntia versicolor* Engelmann ex J.M. Coulter *O. thurberi* Engelmann subsp. *versicolor* (Engelmann ex J.M. Coulter) Felger & Lowe]
Staghorn cholla; *sivirı*. Figure 13.

Chollas reaching 2–2.5 m tall with an open branching pattern, the stems become greenish purple in winter and dry seasons. Joints firmly attached, generally 5–15 cm long, the tubercles prominent. Inner tepals probably 2–2.5 cm long and variously colored (see below), filaments yellow-green, the anthers yellow. Flowering April and May. Fruits probably 2.5–4 cm long, fleshy, greenish, sometimes tinged with purple, persistent through most of the year, and often several clustered at a stem tip.

Figure 13. *Cylindropuntia versicolor*. Kitt Peak Road near Hwy 86 (A) 25 May 2010, (E & F) 28 Apr 2006. (B & C) Hwy 86 west of Quijotoa, 30 Apr 2005. (D) San Simon Valley, Hwy 86 E of San Simon, 6 Nov 2013.

A few, small, scattered populations are documented in Arizona Upland areas of Organ Pipe, where this cholla is at its westernmost limit and rare.

This cholla is common across much of southern Arizona but east of the flora area. South-central Arizona and Sonora southward to the Guaymas region. Flower buds and young stems were cooked and the fleshy fruits were eaten fresh (e.g., Castetter & Underhill 1935).

In southern Arizona the flowers can be yellow, yellow-green, or reddish, including the Tucson Mountains (the type locality) westward to the Kitt Peak Road area and elsewhere along Hwy 86, including the San Simon Valley. Farther south in Sonora the flowers are consistently yellow to yellow-green. Putative hybrids between *C. versicolor* and *C. acanthocarpa*, *C. leptocaulis*, and *C. spinosior* have been reported from outside the flora area (Grant & Grant 1971; Pinkava 2003a).

OP Just W of Diablo Mts along Ajo Mt Drive, 650 m, 32°00'30"N, 112°44'W, 16 May 1989, *Baker 7752* (ASU). 0.2 m S of intersection of road to Cabeza Prieta Game Refuge on Bates Well Road, 3 Dec 1990, *Felger 90-579* (ARIZ, ASU)

Cylindropuntia cf. whipplei, see **Cylindropuntia multigeniculata**

Echinocactus

Barrel cacti, solitary or branched basally, with stout spines, diurnal flowers, and fruits mostly dry when ripe and conspicuously woolly. A genus of seven species in Mexico and southwestern USA; three species occur in Arizona including *E. horizonthalonius* Lemaire and *E. xeranthemoides* (J.M. Coulter) Engelmann (*E. polycephalus* var. *xeranthemoides* J.M. Coulter).

Echinocactus polycephalus Engelmann & J.M. Bigelow
Many-headed barrel cactus, cottontop cactus; *biznaga*. Figure 14.

Multiple-headed barrel cacti, 0.5–1 (2) m wide, the plants often with 6–50 (100+) stems or "heads." (A giant mound-shaped plant on a sandy plain near the western boundary of Cabeza Prieta measured 190 × 201 cm wide, 81 cm tall, and had more than 152 stems; Figure 14A.) Individual stems 9–12 (19) cm diameter. Spines nearly obscuring the stem surface, very stout, rigid, straight to slightly curved near the tip and often twisted but not hooked, ridged below to flattened, the central spine especially stout, often 5–8.5 cm long. Spine surfaces red but obscured by felt-like covering of overlapping, short, white hairs imparting a dull pinkish gray color. Young areoles densely white woolly, older areoles less so. Flowers about 5.5 cm long, confined between the dense spines and thus not opening fully, the inner tepals 2.4–2.6 cm long, the interior of the flower bright, clear yellow (inner tepals, stamens, stigma, and style), the outer tepals bristle-tipped and yellow with a reddish midstripe. Fruits densely and persistently white woolly, drying soon after maturity; fruits plus the persistent, aristate outer tepals 3.5–4 cm long. Seeds blackish (dark red-brown under magnification and bright light), (3) 3.5–4 mm maximum diameter, with a low ridge or crest, the seed surface papillate and often angled due to compression at time of development. Flowering late May and June.

Central and southwestern part of Cabeza Prieta and the Tinajas Altas region; sand flats and sandy soils of valley floors, rocky flats especially on desert pavements, bajadas, and sometimes in soil pockets among hills and lower slopes.

The short, white hairs on the spines suddenly become translucent when wet, revealing the blood-red spine surfaces (Figure 14C): the spines are red in the rain, but revert to their usual dull color when rain ceases. The flowers are confined by the dense spine cover and for this reason do not open as wide as most other cactus flowers. The dry, seed-bearing fruits are likewise tenaciously held among the closely set spines and may remain in place for one year or more. The seeds fall as the fruits disintegrate. The plants generally flower profusely but in at least some years set few fruits. We

Figure 14. *Echinocactus polycephalus*. (A) Richard B. Laugharn and a plant with 152 stems, sandy plain in W margin of Cabeza Prieta, 28 Mar 2010, photo by Richard Felger. (B, E & F) Spine cluster and fruits, near Red Cone, Pinacate Biosphere Reserve, Sonora, 18 Jan 2009. (C) Wet spines, vicinity of Tinajas Altas, 22 Nov 2008, photo by Richard Felger. (D) Anza Borrego Desert State Park, San Diego Co., CA, photo by Bill Sullivan for ABD Natural History Assoc.

have not seen seedlings or small juvenile plants in the flora area, and presumably recruitment is a rare event.

Echinocactus, probably *E. polycephalus*, has been in the Tinajas Altas region for more than 43,000 years. Evidence from the fossils indicate these plants were more common on rocky slopes than today, which is more like the habitat of the Grand Canyon population, *E. xeranthemoides*, than that of *E. polycephalus*.

Echinocactus polycephalus is confined to some of the hottest, driest areas of the Sonoran and Mohave Deserts in northwestern Sonora, southwestern Arizona, southern Nevada, and southeastern California. It is replaced by *E. xeranthemoides* (J.M. Coulter) Engelmann (*E. polycephalus* var. *xeranthemoides* J.M. Coulter) to the north in Nevada and the Grand Canyon region in Arizona (Salywon & Hodgson 2012).

Some people in Yuma call it the "cannonball cactus." Large and small plants alike seldom re-establish after transplanting, and attempts to cultivate it in Tucson and Phoenix fail, probably due to too much rainfall. Sliced pieces of the stems were eaten, often boiled or pit-baked, by Hia C'ed O'odham and others. In "modern" times (probably during the first half of the twentieth century) the stems were made into cactus candy (Bean & Saubel 1972; Hodgson 2001; Zepeda 1985). The flower buds and seeds were eaten by the Cahuillas and others (Barrows 1900; Coville 1892).

Michele Lanan (pers. com. to Felger, 23 May 2014) verified extrafloral nectaries in *E. polycephalus* in late January 2014, in Inyo Co., California, at several sites along the Death Valley Road/Loretta Mine Road, from Big Pine along Hwy 190 to Death Valley. She observed numerous plants; some individuals had no nectaries, while others had a few per areole with ants near the stem apex. The presence of ants in January indicates some *E. polycephalus* EFNs might be active all year like those on *Ferocactus wislizeni*.

CP: 3.5 mi NE of Tule Well, low hills with desert pavement and very sparse vegetation, *Carnegiea gigantea, Fouquieria splendens, Larrea divaricata, & Olneya tesota*, 14 Jun 1992, *Felger 92-596* 1.5 mi E of intersection at Tule Well along the Camino del Diablo, 5 Mar 1995, *Rebman 2887* (ASU, DES, UCR, SD).

TA: Tinajas Altas Mts, desert flats SW of mountains, Camino del Diablo (West Route), *Larrea tridentata, Ambrosia dumosa, Cercidium microphyllum, Fouquieria splendens, Olneya tesota, Opuntia ramosissima*, 12 Feb 1977, *Reeves 5426* (ASU). 0.5 km E of Camino del Diablo on road to Borrego Canyon, 4 Feb 1990, *Felger 90-20*. *Echinocactus* cf. *polycephalus*: †Butler Mts, seeds, 3820 to 11,060 ybp (5 samples). †Tinajas Altas, spines, seeds, 9700 to 15,680 (4 samples), & >43,000 ybp

Echinocereus – Hedgehog cactus

Multiple-stem, spiny cacti, branching mostly from the base (those in the flora area). Spines several or more per areole, straight to curved, not hooked; areole glands absent. Receptacle spiny at anthesis, the spines not enlarging during fruit maturation. Flowers showy, medium-sized to large, adapted for daytime pollination, the stigma green. Fruits succulent and spiny, the dried perianth persistent; ripe fruits sweet and delicious, the spines falling away when the fruit ripens. Seeds blackish, tuberculate, rounded to obovoid.

The genus ranges from tropical to temperate regions in Mexico and western United States. The taxonomy is complicated due to fuzzy taxonomic boundaries, polytypic taxa, and differing interpretations by specialists. Most North American botanists recognize about 50 species (e.g., Baker 2012a; Zimmerman & Parfitt 2003a), while the *Echinocereus* specialists in Germany recognize more than 70 species (e.g., Blum et al. 1998).

1. Longer spines often 2.5–4 (5) cm, spines of a single color (straw-colored to gray); flowers red to red-orange; higher elevations in the Ajo Mountains. ..... **Echinocereus coccineus**
1. Longer spines usually 4–10 cm, the central spine(s) similar or different in color from the radial spines; flowers pink or purplish; widespread.

2. Spines dull yellow, brownish, and grayish, often bicolored, becoming (or remaining) gray (rarely blackish) with age; flowers usually deep magenta, very showy; seeds 1.3–1.5 mm long..... **Echinocereus engelmannii**
2. Spines uniformly yellow, often blackish with age; flowers usually pale pink; seeds 1.1–1.3 mm long. ..... **Echinocereus nicholii**

Echinocereus coccineus Engelmann subsp. **santaritensis** (W. Blum & Rutow) M.A. Baker, **comb. et stat. nov.** *Echinocereus santaritensis* W. Blum & Rutow, in W. Blum, M. Lange, W. Rischer, & J. Rutow, Echinocereus Monographie [Fa. Proost, Turnhout, Belgium], 373–375, 1998. Herbarium for the holotype corrected from UA to ASU in Der Echinocereenfreund 12: 93, 1999.

Santa Rita claret-cup cactus. Figure 15.

Multiple-stem hedgehog cactus usually branching from the base. Stems generally less than 30 cm long and average 5.5 cm wide, generally with 9 or 10 ribs, rather densely spiny, with the areoles on the same rib about 1 cm apart. Spines straw-colored to gray, each spine of one color, generally 3 or 4 centrals and about 10 radials per areole, longest centrals 2.5–4 (5) cm (generally ca. 3 cm long) and 0.6 mm thick. Flowers moderately bilaterally symmetrical (moderately zygomorphic), 5–11 cm long, 3–4 cm wide, bisexual, with a long style averaging 5 cm long, the inner tepals bright red to orange-red, flowering in April. Tetraploid, $2n = 44$ (Baker 2006).

Ajo Mountains above 1070 m on bedrock cliffs, cliff ledges, rocky slopes, and boulder outcrops, often growing near *Juniperus arizonicus* and *Vauquelinia californica*. This is the westernmost locality for subsp. *santaritensis*.

Subspecies *santaritensis* is widespread in mountains eastward in southern Arizona including the Atacosa, Chiricahua, Huachuca, Pajarito, Patagonia, Pinal, Pinaleño, Santa Catalina, Santa Rita (type locality), and Tucson Mountains, and in adjacent north central and northeastern Sonora.

The *Echinocereus coccineus* complex includes about one half dozen red-flowered, tetraploid and hexaploid species or infraspecific taxa. These are mostly montane cacti in Arizona, Colorado, New Mexico, Texas, and Utah, and southward in the Sierra Madre Occidental to Jalisco, and in northern Baja California. The differences between *E. santaritensis* and *E. coccineus* subsp. *coccineus* intergrade over an extensive geographical range in central Arizona, which suggests that *E. santaritensis* is better placed as a subspecies of *E. coccineus*. Most populations of *E. coccineus* subsp. *coccineus* have at least some individuals with pollen-sterile flowers, while those of *E. coccineus* subsp. *santaritensis* have only individuals with bisexual flowers. Flowers of *E. coccineus* subsp. *santaritensis* have mostly long styles (5 cm) and the areoles of the pericarp possess hairs that are longer than the subtending scale leaf, while those of subsp. *coccineus* have styles less than 4 cm long and the areoles of the pericarp have hairs that are shorter than the subtending scale leaf.

Echinocereus santaritensis has been listed as synonym of *E. polyacanthus* Engelmann by Anderson (2001). According to Sánchez et al. (2013), populations of *E. polyacanthus* are restricted to north-central Mexico. Although the areoles of the pericarpel in both species have long hairs that exceed the subtending leaf, flowers of *E. polyacanthus* are short and polymorphic (some individuals with pollen-sterile flowers and some with pollen-fertile flowers), while the flowers of *E. santaritensis* are long, pollen fertile and probably always perfect.

OP: 1.7 km S of Mt Ajo, 3600 ft, NW-facing cliffs of pink-brown rhyolite, associated species: *Achnatherum speciosum, Acourtia wrightii, Agave deserti, Aloysia wrightii, Artemisia ludoviciana, Crossosoma bigelovii, Cylindropuntia acanthocarpa, Echinocereus mcholii, Enogonum wrightii, Ferocactus emoryi, Fouquieria, Gnaphalium canescens, Juniperus coahuilensis, Mammillaria grahamii, Notholaena standleyi, Opuntia chlorotica, Pellaea truncata, Rhamnus crocea, Simmondsia chinensis, Vauquelinia californica, and Viguiera parishii;* locally approx. 10 individuals, generally on inaccessible shelves and cliff faces, 27 Apr 2001, *Baker 14050* (ASU). N-facing slope above Bull Pasture, 10 Apr 2005, *Rutman 2005-0410-21* (ORPI)

AZ: **Santa Cruz** Co.: "*Echinocereus coccineus* Engelm., *sensu lato* (including *E. polyacanthus* Engelm.), det. Allan D. Zimmerman, February 1997. Plant and unattached flowers presented to Zimmerman in 1996 with the following field data: . . . Santa Rita Mountains. Coronado National Forest, Madera Canyon . . . . ca. 1650—1700 m . . . mostly in bud, flowers widely open at 10:30 a.m., 16 April 1996 (at beginning of

blooming season), Jurgen Rutow & Michael Lange view this collection as the prospective **type** for a taxonomic split (preserved by ADZ in 1996, VOUCHER for a horticultural cutting in ADZ's living research collection), *Jürgen Rutow 52/96*" (holotype of *E santantensis*, ASU 211396, note that the protologue incorrectly indicates the holotype is at "UA," which was later corrected to ASU).

Figure 15. *Echinocereus coccineus* subsp. *santantensis*. Ajo Mts above Bull Pasture, 10 Apr 2005.

Echinocereus engelmannii (Parry ex Engelmann) Lemaire subsp. **engelmannii**
[*E. engelmannii* var. *acicularis* L.D. Benson *E. engelmannii* var. *chrysocentrus* (Engelmann & J.M. Bigelow) Rumpler]
Strawberry hedgehog cactus, *pitayita*, 'ısvigĭ. Figure 16.

Several to many stems branching mostly from near the base, the stems 15–45 cm tall, about 7 cm wide, with a moderate to dense spine cover. Spines dull yellow to brownish, whitish, or grayish, becoming (or remaining) grayish with age, each areole generally bearing spines of various colors. Central spines (2)3–6(9), the longer (lower), central spine 3–10.5 cm long, often becoming whitish

Figure 16. *Echinocereus engelmannii*. (A & D) S of Scarface Mtn, Organ Pipe, 11 Sep 2013. N end of Little Ajo Mts. (B) 27 Mar 2005; (E) dried fruit, 17 Jul 2013. (C) Fresh fruits, Kuakatch Wash near Hwy 85, 23 May 2012.

with age, twisted or straight, flattened or terete, the other spines terete. Flowers showy, 7.5–9 cm long, 5–9 cm wide; inner tepals 4–7.5 × 1.5–2 cm, generally bright purple-magenta (sometimes varying from pink to darker colored in the same population). Fruits at first spiny, the spine clusters falling away at maturity, the pulp infused with pink or red from the red fruit skin. Seeds 1.3–1.5 mm long. Flowering March and early April; fruits ripe late May and early June. Upon ripening the fruit pulp and seeds are promptly consumed by a variety of animals, especially birds that poke a hole in the side of the fruit. Ants quickly finish off what the birds leave, and hollowed-out fruits are common.

Widespread and common across the entire flora area in many habitats, from lowest to high elevations. Usually on rocky substrates but also in deep, sandy-silty soils; mountains, hills, bajadas, desert flats, and sometimes upper floodplains of larger washes. Often growing with *E. nicholii* in the Puerto Blanco Mountains and elsewhere.

Western Arizona, southern California, Nevada, southwestern Utah, Baja California, northeastern Baja California Sur, and northwestern Sonora.

The fruits are delicious and are edible fresh together with the small seeds (Felger & Moser 1985; Rea 1997). The cooked stems were also eaten. "They ate the meat of the hedgehog cactus . . . like potatoes. . . . Shave them and then you cut them . . . and put salt on them" (Betty Melvin in Zepeda 1985: 61). Considerable quantities of seeds were found at a Hohokam site near Phoenix, suggesting cultivation and use as a trade item (Gasser 1982; Gasser & Kwiatkowski 1991).

Varieties defined by Benson (1982) within *Echinocereus engelmannii* (sensu stricto) have little geographical or morphological foundation (Baker 2012a; Zimmerman & Parfitt 2003a). Individuals from lower elevations tend to have stouter spines and larger stems than those at higher elevations. At almost every type locality for names associated with *E. engelmannii* (sensu stricto), morphological variation encompasses two to several varietal descriptions. Populations of *E. engelmannii* subsp. *engelmannii* represent a western form with mostly three or more angled central spines. In central Arizona, it intergrades with populations of *E. engelmannii* subsp. *fasciculatus* (Engelmann ex S. Watson) W. Blum & Michael Lange, which represent an eastern form with one or two terete central spines. All chromosome determinations for *Echinocereus engelmannii* (sensu lato) throughout its range have been $2n = 44$ except for a small region, where it is $2n = 22$, from St. George, Utah to just across the border in Mohave Co., Arizona. No consistent morphological characteristics have been found that differentiate the two chromosome races.

OP: Quitobaquito and vicinity. 5 Mar 1940, *Peebles 14555*, 29 Mar 1988, *Felger 88-112*. Bates Well, 30 Mar 1978, *Bowers 1121*. Puerto Blanco Drive at old road to Dripping Springs, 12 Apr 1978, *Bowers 1256*. Puerto Blanco Mts, 2 km WNW of Dripping Springs, 1720 ft, $n = 22$ (meiotic count), 7 Mar 1988, *Baker 7584* (ASU, SD). N boundary of Monument, 0.2 km W of AZ Hwy 84, 2 Dec 1990, *Felger 90-502*.

CP: Childs Mt, 9 Apr 1993, *Felger 93-280*. Observations, *Felger*. Agua Dulce Pass, Heart Tank, Tuseral Tank, 12 & 14 Jun 1992, Sheep Mt, Sand over lava at E side Pinacate flow, 31 Jan 1992, Tule Tank, 2 Feb 1992.

TA: Tinajas Altas, 15 Apr 1932, *Blackwell 709*. Observations, *Felger*. Ridge above Tinajas Altas Canyon, 19 Mar 1998; Granitic bajada at SW side of Tinajas Altas Mts, 10 Jan 2002

Echinocereus nicholii (L.D. Benson) B.D. Parfitt
[*E. engelmannii* (Parry ex Engelmann) Lemaire var. *nicholii* L.D. Benson]
Golden hedgehog cactus. Figure 17.

Larger plants with 16–24+ stems branching near ground level, forming clumps often reaching 0.50–1+ m wide. Individual stems 6–9 cm diameter, erect to ascending. Spines translucent-yellow, often golden, monochromatic, becoming blackish on older parts of the stem; central spines 4–6, the longer ones 4–7 cm long, often twisted and somewhat flattened. Flowers generally pink, smaller and

much paler than those of *E. engelmannii* (sometimes varying from pink to magenta in the same population). Fruits ovoid, 2.3–3.4 × 1.7–2.3 cm, remaining spiny after ripening, the skin green, becoming somewhat bronze when fully ripe where exposed to sunlight, the pulp remaining whitish. Seeds 1.1–1.3 × 0.8–1.2 mm. Flowering March and April, the fruits ripening in June. $2n = 22$.

Mostly on steep rocky slopes and hills, often very common towards higher elevations, sometimes on pediments at the base of rocky hills, and especially on bedrock or other stable substrates with very little soil. Widespread in the mountains of Organ Pipe including the Ajo, Growler, Puerto Blanco, and Quitobaquito Mountains, and in the eastern part of Cabeza Prieta. The north side of Sheep Peak in the Growler Mountains in Cabeza Prieta supports an exceptionally dense and extensive population. It is not found on bajadas or valley bottoms. Often most numerous on north-facing slopes and growing with *E. engelmannii* as well as *Carnegiea gigantea*, *Cylindropuntia acanthocarpa*, *Ferocactus cylindraceus*, *F. emoryi*, *Mammillaria grahamii*, *Stenocereus thurberi*, and sometimes *Sclerocactus johnsonii*.

Southern Arizona eastward from our flora area to the Silverbell and Waterman Mountains west of Tucson and western Sonora southward to the Sierra Seri (opposite Isla Tiburón).

The fruits were eaten together with the seeds by Hia C'ed O'odham (Hodgson 2001), probably as a minor food resource. Hodgson (2001) found the fruits to be even sweeter and better-tasting than other hedgehog cactus fruits (Felger 2007).

Figure 17. *Echinocereus nicholii*. (A) Growler Canyon, Bates Mts, 9 Sep 2012. (B) Growler Mine, Bates Mts, 13 Sep 2013. (C) Middle Fork of Alamo Canyon, Ajo Mts, 26 Mar 2005.

Echinocereus nicholii is distinguished from *E. engelmannii* by its generally larger and more robust habit, monochromatic yellow spines that become blackish with age, smaller and pink flowers, and different seed morphology. (*Echinocereus nicholii* occasionally has flowers larger and darker than usual and somewhat resembling those of *E. engelmannii*.) Also, for all individuals tested within the flora area, those of *E. engelmannii* have been tetraploid and those of *E. nicholii* diploid.

OP: 1 mi E of Bates Well, 4 Mar 1940, *Benson 9901*. Alamo Canyon, 14 Mar 1941, *Benson 10672*. Bull Pasture Trail, 1 Apr 1978, *Bowers 1234*. 2.4 mi W of Hwy 85 on Puerto Blanco Drive, 19 Jun 1989, *Felger 89-220*. Quitobaquito Hills, 22 Feb 1990, *Felger 90-39*. Gunsight Hills, 2 Mar 2003, *Rutman 2003-206* (ORPI). Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger* (observation).
CP: Childs Mt, 2240 ft, 9 Apr 1993, *Felger 93-280*. Observations, *Felger*: Sheep Peak, N side at higher elevations, not on S-facing slopes except at summit, 31 Jan 1992; Agua Dulce Pass, 12 Jun 1992.

†**Echinocereus** sp./spp.

All but one of the fossil samples are from the Middle to Late Wisconsin age in the Ajo and Puerto Blanco Mountains. They are perhaps members of the *E. coccineus* complex, or the youngest samples might be one of the other two present-day *Echinocereus* species.

OP: †Alamo Canyon, seeds, 1150 to 29,110 ybp (3 samples). Montezuma's Head, seeds, 13,500 & 21,840 ybp. Puerto Blanco Mts, on ridge, seeds, 2340 ybp.
TA: †Tinajas Altas, seeds, 1030 to 10,600 (5 samples), & >37,000 ybp.

Echinomastus, see **Sclerocactus**

Ferocactus – Barrel cactus; *biznaga*; jiavul

Three barrel cactus species occur in Arizona. These have a single stout stem (rarely 1 or few branches if the apical meristem is injured). Areoles at the stem apex have short hairs forming a felt-like indumentum and areoles near the top of the stem have smooth, conical, yellowish brown extrafloral nectaries tended by ants (e.g., Lanan & Bronstein 2013; Morris et al. 2005; Ness et al. 2006; Ruffner & Clark 1986). Flowers yellow, orange, or red. Fruits fleshy, ripening after a number of months; the dried perianth persistent on the fruits; fruit rind yellow-green when immature, yellow when ripe, the pulp (funiculi) white. Although the fruits do not dehisce spontaneously, a fruit removed from the plant is like a saltshaker, scattering seeds from a hole at the base (where the fruit was attached). Seeds blackish, smooth or pitted. Many animals feed on the fruits, including ground squirrels that often scamper up the spines to munch the fruits. $2n = 22$.

The genus includes about 25 species, southwestern United States from California to Utah and Texas and Mexico southward to Oaxaca.

People across the Sonoran Desert made use of these large cacti. The flower buds and flowers were cooked and sometimes dried and stored. The cooked buds and flowers have a flavor somewhat like that of Brussels sprouts. Sometimes the buds were eaten fresh, although they are bitter unless cooked. The seeds, rich in oil and protein, were ground into an oily paste. The fresh fruits are edible but very acidic or sour (Bean & Saubel 1972; Felger & Moser 1985). Barrel cactus stems were baked in a pit, and the "meat" sliced and eaten or the "pulp" otherwise cooked (Castetter & Underhill 1935; Rea 1997; Melvin in Zepeda 1985: 49). Palmer (1878) reported that Tohono O'odham boiled pieces of the pulp in saguaro or organ pipe fruit syrup. Emergency liquid can be extracted from *F. cylindraceus* and *F. wislizeni* stems, but according the Seris the juice from *F. emoryi* is highly toxic (Felger & Moser 1985; Hodgson 2001) and presumably stem tissue or liquid of that species would not be ingested, at least not uncooked.

"They would gather it, and cut the skin off, and cut up, slice up, the meat of the barrel cactus, and they would cook it, they would roast it inside a pit sometimes, and then more recently they made candy out of it, the cactus candy" (Betty Melvin in Zepeda 1985: 49, 58). "You can cut the meat of the barrel cactus and you can suck the water from it. . . . my cousin Willie told me. . . one time he and his friends were out hunting in the desert. . . and this animal [probably a desert bighorn] would ram into the cactus and break the skin of the cactus and busted the cactus down. They watched him and he started to lick and eat the meat of the cactus." For medicine, "that hivijuls, if you have a sore you take it. . . . When it is not hard yet, you put it on the sore. If the plant is hard, you boil it and then wash the sore with it. The sore will get better quickly" (Betty Melvin in Zepeda 1985: 80).

The barrel cactus species in our flora sometimes reach 1.5–1.7 m in height, but in more equable (less xeric) regions they sometimes reach 3 m in height (Lindsay 1955, 1996; Zimmerman & Parfitt 2003b). A methuselah fishhook barrel cactus (*F. wislizeni*) south of Tucson measured 11.5 ft (3.5 m) in height with a maximum diameter of 3.5 ft (1.07 m) (Pima Co., San Luis Mts, SSW of Arivaca, 3750 ft, *Peachey 15 Dec 1994*, ARIZ 315928).

1. Spines all robust and rigid, more or less uniform in thickness (none are bristly) ..... **Ferocactus emoryi**
1. Spine clusters with slender, bristle-like spines in addition to the thick, rigid spines.

2. Stem growing straight up; largest spines hooked or not, often markedly twisted; seed surfaces pitted, resulting in a conspicuous reticulate pattern; rocky substrates (hills and mountains)..... **Ferocactus cylindraceus**
2. Larger plants usually conspicuously leaning southward; largest spines in each areole usually hooked, seldom twisted; seed surfaces essentially smooth and only minutely reticulate; flats and open desert..... **Ferocactus wislizeni**

Ferocactus cylindraceus (Engelmann) Orcutt
[*Echinocactus viridescens* var. *cylindraceus* Engelmann. *Ferocactus acanthodes* (Lemaire) Britton & Rose (an ambiguous name, Taylor 1979 and Zimmerman & Parfitt 2003). Not *Echinocactus acanthodes* Lemaire]
Desert barrel cactus. Figure 18.

Stem cylindrical, growing straight and erect, the larger plants taller than wide; flowering plants (20) 45–125 cm tall (sometimes to 150 cm in the hills above Quitobaquito), (20) 25–38 cm diameter. Young plants (to about 15 cm tall) often with 14 stem ribs, adult plants with 19–20 ribs. Central spines whitish, gray, pink, or dull red (bright red when wet) with yellow-white tips, or sometimes straw-yellow with broad red or pink bands. Central spines moderately curved, sometimes twisted, usually not strongly hooked (except on immature plants); longer central spines 4–8.5 cm. Areoles with 4 major thick, rigid central spines, these surrounded by smaller spines (subcentrals or large radials, depending on interpretation), these rigid and intergrading with the centrals; radials (outermost spines) mostly bristle-like. Flowers often about 4.5 cm long (smaller than those of the other two *Ferocactus* in the region); inner tepals pure yellow to more often yellow with a salmon to maroon midstripe, orange, or sometimes red and with a darker red midstripe. Filaments reddish or yellow. Anthers, style and stigma lobes yellow (including otherwise red flowers), pale red, or red-magenta. Seeds pitted. Usually flowering February–April, and less vigorously late summer–early fall.

Widespread and often common on rocky hills and mountain slopes, at all elevations in Cabeza Prieta, parts of the Tinajas Altas Mountains, and the drier mountains in Organ Pipe. Growing on various slope exposures but mostly on west- and south-facing slopes. Barrel cacti are scarce in the vicinity of the waterholes in the western part of the flora area, such as at Tinajas Altas and Surveyors

Tank in the Tinajas Altas Mountains and also at higher elevations above the waterholes. In these places most of the larger individuals occur on inaccessible cliffs and rock faces. Their scarcity near

Figure 18. *Ferocactus cylindraceus*. (A) Gunsight Hills near Hwy 85, 15 Apr 2012. Near Red Cone, Pinacate Biosphere Reserve, (B) 7 Mar 2009, (C) Garden in Ajo, 21 May 2006, (D) spines of a young plant, 10 May 2005 (*F. cylindraceus* is the only barrel species at Red Cone and elsewhere in the Sierra Pinacate, Felger 2000), (E) Granitic hill, W end of Javelina Mtn, Sand Tank Mts, Maricopa Co, 5 Mar 2005.

the tinajas is undoubtedly due to bighorn sheep, which dislodge the plants with their horns and eat the fleshy stem (e.g., Warrick & Krausman 1989). This barrel cactus has been in the flora area for more than 11,000 years. It was at least reasonably common in the Tinajas Altas region from about 11,000–3800 years ago, but its absence in younger middens indicates a decline in abundance and it is still locally not common.

Populations in the flora area and nearby northwestern Sonora show the following patterns: Those in volcanic regions, on darker lava rock are characterized by elongated, twisted, stout, and reddish to pink or gray spines; some have bright yellow inner tepals, most are orange or yellow with a red midstripe, and some have bright red-orange to red inner and outer tepals. Plants on granitic hills and mountains generally have dull-colored, mostly straw yellow, and relatively shorter and more slender spines, consistently yellow inner tepals, and yellow or somewhat reddish filaments.

Southeastern California, southern Nevada, southwestern Utah, western Arizona, Baja California, and northwestern Sonora.

Across most of its geographic range this species characteristically occurs on rock slopes, where the plants are firmly anchored in rock or rocky soils and the plants grow straight up and not leaning like those of *F. wislizeni*. There is considerable variation in spine size and shape, and spine and flower color, but the colors and other features are apparently consistent within a local population and correlated with rock type. Benson (1982) recognized three varieties in the USA and one in Baja California. Zimmerman and Parfitt (2003b: 246) stated, "The varieties recognized by L.D. Benson are not consistently distinguishable." Others disagree and recognize all or some of the varieties: cactus taxonomy is fluid and fun.

OP: Near Bates Well, 4 Mar 1940, *Benson 9895*. Quitobaquito Hills, 12 Sep 1988, *Felger 88-456*. †Puerto Blanco Mts, on ridge, seeds, 1910 to 9720 ybp (7 samples).

CP: 7 mi E of Papago Well, 15 Mar 1937, *Harbison 16848* (SD). Tule Tank, 1300 ft, 15 Apr 1941, *Benson 10809*. T13S, R14W, S24, 6 Apr 1969, *Lehto L23489* (ASU). Observations, *Felger*. Agua Dulce Pass, Buckhorn Tank, Cabeza Prieta Tanks, Eagle Tank, 13–15 Jun 1992. 3 1 mi W of Tule Well on Camino del Diablo, 5 Mar 1995, *Rebman 2885* (DES).

TA: Borrego Canyon, 3 Feb 1990, *Felger 90-5*. Slopes at Tinajas Altas, 19 Mar 1998, *Felger* (observation). †Butler Mts, spines, seeds, 3820 to 11,250 ybp (5 samples). †Tinajas Altas, seeds, 4010 to 10,070 ybp (10 samples).

Ferocactus emoryi (Engelmann) Orcutt, Cactography 1926 (1): 5, 1926.
[*Echinocactus emoryi* Engelmann, Proc. Amer. Acad. Arts 3: 275, 1856, "Lower Colorado, and principally in Sonora." *Ferocactus covillei* Britton & Rose, Cactaceae 3: 132–133, f. 138–139, 1922, "Sonora, hills and mesas near Altar," 11 Aug 1884, *C.G. Pringle s.n.* (F). *Ferocactus emoryi* subsp. *covillei* (Britton & Rose) D.R. Hunt & Dimmitt, Cact. Syst. Initiat. 20: 16, 2005 (basionym not cited, and name re-published in Cact. Syst. Initiat. 21: 11, 2006)]
Emory barrel cactus, strawberry barrel. Figure 19.

Plants 0.6–1.7 m tall, the stem often 30+ cm diameter, with 21 ribs. Spines all rigid and stout (bristle-like spines not present); central spines 5.5–9.5 cm long (not including curve), hooked on smaller, immature plants and curved but not hooked on mature plants. Flowers often 7.5 cm wide; inner tepals, filaments, style, and stigmas red to red-orange; stigma 16-lobed. Seeds conspicuously pitted. Flower buds produced beginning in early March and flowering (July) August to mid-September; flowers highly fragrant.

Scattered on rocky slopes of hills and mountains, middle to upper bajadas, and occasionally on lower bajadas, plains, and sandy flats. Eastern part of Cabeza Prieta in the Agua Dulce and

Growler Mountains and widespread across Organ Pipe including the Ajo Mountains to higher elevations. It has a 3500-year history in Organ Pipe.

Southwestern Arizona and western Sonora southward to the coastal Yaqui lands southeast of Guaymas, and reported to extend southward to northwestern Sinaloa in the vicinity of Topolobampo (Taylor 1984, Unger 1992).

There are two color-specific populations: a red-flowered northern population and a yellow-flowered southern population. The northern race, in the Sonoran Desert north of Hermosillo and Bahia Kino, Sonora, to southern Arizona, predictably has red to red-orange flowers. The southern race, from the Guaymas–San Carlos region at the southern edge of the Sonoran Desert and southward

Figure 19 *Ferocactus emoryi*. (A & B) Ajo, 31 Jul 2013. (C) N of Bates Mts, 11 Sep 2013. (D & E) Alamo Canyon, Ajo Mts, 5 Nov 2013. (F) Juvenile plant, Javelina Mtn, Sand Tank Mts, 5 Mar 2005.

in Sonora in thornscrub, predictably has bright yellow flowers. The population bridging the northern and southern race, in the Sierra Libre, between Guaymas and Hermosillo, has the full span of yellow, orange, orange-red, or red flowers, and all three colors sometimes occur even on a single plant (Paredes et al. 2000). The southern, yellow-flowered population has been named *F. emoryi* subsp. *covillei* (Britton & Rose) D.R. Hunt & Dimmitt. The type locality for *F. covillei* Britton & Rose, however, is in northwestern Sonora, in midst of the range of the red-flowered, northern population. Hunt and Dimmitt's subsp. *covillei* therefore does not match the definition of having a separate range for a subspecies. According to the prevailing definition, a subspecies is recognized by having a separate range, i.e., separate from the proposed nominate subspecies.

Felger and Zimmerman (2000) disagreed with Taylor (1984) that *F. rectispinus* (Engelmann ex J.M. Coulter) Britton & Rose should be treated as a variety of *F. emoryi*. *Ferocactus rectispinus*, endemic to Baja California Sur, is morphologically and geographically clearly isolated from *F. emoryi*. The basionym, published in 1896 as *Echinocactus emoryi* var. *rectispinus* Engelmann ex J.M. Coulter, shows that Taylor was not the first to make an association of the two species, although neither Engelmann nor Coulter saw the plants in the field (see Lindsay 1955, 1996).

OP: Quitobaquito, *Nichol 28 Apr 1939* (ORPI). E of Bates Well, 4 Mar 1940, *Benson 9896*. Twin Peaks, 3 Dec 1989, *Pinkava 14371* (ASU). Observations, *Felger*. W of Hwy 85 at N boundary of Monument, 23 May 1991; Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005. †Puerto Blanco Mts, on ridge, spines, seeds, modern (30) to 3480 ybp (8 samples).

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 16849* (SD). Bajada, near wash, 19 Mar 1975, *Lehto L18392* (ASU). Observations, *Felger*. Adobe Windmill, W end of Agua Dulce Mts, S side of Growler Pass, 12 & 13 Jun 1992; Childs Mt, 2400 ft, 18 Aug 1992.

Ferocactus wislizeni (Engelmann) Britton & Rose
[*F. wislizeni* subsp. *ajoensis* Fencl & Kalas, Bradleya 31: 7–11, f. 3–6, 8–11, 2013]
Compass barrel cactus, fishhook barrel cactus. Figure 20.

Plants mostly less than 1 m tall, some reaching 1.5 m, the stem very thick, often 35–65 cm diameter; stem ribs often 21–27. Larger plants usually conspicuously leaning (growing) southward. Spines dull gray, the larger spines strongly hooked, longest central spines of adult plants (from curve of hook to base) 6–8.5 cm; outer radial spines slender and bristle-like. Younger plants to about 15 cm tall have markedly longer spines than larger, adult plants; longest central spines often reaching 12 cm. Extrafloral nectaries prominent in the proximal (adaxial) portion of young areoles and actively tended by ants all year. Flowers often 7–8 × 5–7 cm, exceeding the spines, yellow-orange to red-orange, or yellow overall, the inner tepals with an orange-red to red midstripe grading to yellow-orange to yellow on margins, or sometimes the inner tepals bright yellow (all colors between yellow and red-orange are common, including plants next to each other). Filaments pink to red. Seeds essentially smooth with only a slightly raised reticulate pattern. Ants often carry away seeds from hollowed but still fleshy, yellow fruits. Flower buds produced from early March and flowering generally in (late July) August and September; flowers highly fragrant.

Widely scattered in Organ Pipe on sandy gravelly soils of desert plains, lower alluvial flats, and lower to middle bajadas, and thinly and unevenly scattered across much of Cabeza Prieta, mostly valley floors on sandy soils. We have not found this cactus westward from the southern end of the Sierra Pinta in Cabeza Prieta with exception of a single plant at the southeastern corner of the Tinajas Altas region. Soil erosion commonly undermines larger, older plants, especially when growing along the margins of small washes, causing them to topple over and eventually perish. Javelinas sometimes push over the plants and then get into the plant from the bottom to eat the pulp. Sue Rutman says the pulp of this barrel cactus tastes like a cross between a potato and cucumber. This cactus has been in Organ Pipe for at least 10,500 years.

Southwestern and central Arizona to western Texas and adjacent Chihuahua and northern Sonora.

The mutualistic relationships involving ants and the extrafloral nectaries of this barrel cactus has been the subject of extensive ecological investigations, most notably beginning with the work of Judith Bronstein, her lab at the University of Arizona, and colleagues (e.g., Ness et al. 2006; also see *Ferocactus* generic description above).

We find no infraspecific taxon of *F. wislizeni* worthy of recognition. Fencl and Kalas (2013) described the western populations as subspecies *ajoensis*. Their slender forms of the western populations represent the sort of random morphological variation that, if recognized, would lead to a plethora of subspecific taxa. They state that subspecies *ajoensis* has denser spination and larger spines than subsp. *wislizeni*. There may be a trend of larger and stouter spines westward across the species range, but the examples shown for subsp. *ajoensis* appear to be young plants that characteristically have larger and stouter spines than older, larger plants. The authors also state that the flowers are red to orange in subsp. *ajoensis* and yellow in subsp. *wislizeni*. Both flower colors, however, are common across the west–east range of the species.

Felger and Zimmerman (2000: 211) report: "Contrary to a statement by Taylor (1984: 34), we find no evidence that *F. wislizeni* in the southern part of its range . . . intergrades with" the related *F. herrerae* J.G. Ortega. Taylor's statement, however, is from George Lindsay's dissertation (1955; reprinted in Lindsay 1996). There is an eco-geographic gap of perhaps more than 200 km between the southernmost population of *F. wislizeni* in northern Sonora and the northernmost *F. herrerae* in the vicinity of Guaymas, Sonora. Although Taylor and Clark (1983) found little difference in the seeds, the several vegetative differences are conspicuous and consistent. *Ferocactus herrerae* occurs primarily in coastal thornscrub of southwestern Sonora and Sinaloa. In comparison to *F. wislizeni*, *F. herrerae* grows spectacularly fast in cultivation. We also consider *F. tiburonensis* (G.E. Lindsay) Backeberg (*F. wislizeni* var. *tiburonensis* G.E. Lindsay) on Isla Tiburón and the Sonora coast to be a distinct species. *Ferocactus tiburonensis* and *F. wislizeni* are clearly allopatric with no known plants with intermediate morphology (Felger & Wilder 2012).

Ferocactus wislizeni is locally distinguished from *F. cylindraceus* in part by its relatively dull gray, strongly hooked spines, much thicker stems, and general tendency to lean (grow) southward. Zimmerman and Parfitt (2003b) report that claims of hybrids between *F. cylindraceus* and *F. wislizeni* are not substantiated. *Ferocactus cylindraceus* and *F. wislizeni* generally occupy different habitats and are only occasionally found growing together in Arizona beyond our flora area (see *F. cylindraceus*). *Ferocactus wislizeni* occasionally grows with *F. emoryi*, although they generally occupy different habitats. Both species have similar-appearing flowers and may flower at the same time, although in the flora area *F. wislizeni* mostly has orange to orange-red or yellow flowers and *F. emoryi* has deeper red flowers; the spination, however, is clearly distinctive in *F. emoryi*.

OP: Walls Well, *Nichol 2 May 1939* (ORPI). Sandy soil, Growler Mts near Bates Well, 4 Mar 1940, *Benson 9895*. Quitobaquito, 14 Sep 1988, *Felger 88-444*. Hocker Well, 3 Dec 1990, *Felger* (observation). †Puerto Blanco Mts, on ridge, spines, seeds, 3480 to 10,540 ybp (5 samples).

CP: 7 mi E of Papago Well, 20 Mar 1937, *Harbison 16847* (SD). Observations *Felger*: Between San Cristobal Wash and Agua Dulce Mts, 31 Jan 1992; Sand over lava in the Pinacate flow, with *Larrea*, near O'Neill's Grave, Papago Well, 31 Jan 1992; Near Salt Well, 12 Jun 1992.

Figure 20. *Ferocactus wislizeni*. Why: (A) 20 Aug 2006, (E) Why, 8 Aug 2013. (B) Bates Well Road, Organ Pipe, 29 Feb 2008. (C) Gunsight Hills near Hwy 85, 17 Oct 2013, (D) Gachado line camp, 20 Aug 2006. Armenta Ranch Rd near Hwy 85: (F) 17 Oct 2013, (G) 2 Aug 2013. (H) Central spine, Crater Range E of Hwy 85, 7 Jan 2014, (I) Ant (*Crematogastor opuntiae*) visiting extrafloral nectary, Tumamoc Hill, Tucson, 4 Apr 2003, photo by William G. Wilson.

TA: About 2.5 mil SE of Tinajas Altas, Lechuguilla Valley floor near the head of Coyote Wash, 1065 ft, 1 Apr 2011, *Pete Sundt*, observation, from Sundt's vegetation survey plot, species list from the plot, in decreasing abundance: *Ambrosia dumosa, Larrea divaricata, Prosopis glandulosa, Grusonia wrightiana, Lycium fremontii, L. macrodon, L. parishii, Carnegiea gigantea, Encelia farinosa, Echinocactus polycephalus, Hilaria rigida, Asclepias subulata*, and one lonely *Ferocactus wislizeni* (see Felger et al. 2012 for description of the habitat and flora).

Grusonia – Club cholla, dog cholla, *perrito*

Low-growing opuntioid cacti forming colonial colonies, the stems more or less cylindrical-club-shaped, upright, rounded in cross-section but with prominent tubercles, remaining green all year. Stem segments (joints) firmly attached and separable only by tearing the woody axis. Stem and floral areoles each with one small, deciduous tubular-conical leaf; areoles with spines and usually with at least some glochids, sometimes absent in older stems, especially in *G. wrightiana*; spines whitish to gray (reddish or salmon-color when first developing), the larger spines very sharp, rigid, flattened with razor-like margins, mostly pointing downward; spines with a minute and soon-deciduous spine sheath only at the tip of young spines. Flowers one to several at stem tips, outer tepals reddish or pink, the inner and larger tepals whitish or pale yellow. Filaments green, especially near their bases; anthers white to pale yellow. Fruits fleshy, greenish or yellow when ripe and usually soon drying. (The fruits seem to dry sooner during drought conditions than during times of higher soil moisture.)

Grusonia includes 15 species in southwestern USA and Mexico. Four species occur in Arizona (figure 21). As explained below, we consider the club cholla in the flora area previously called *Grusonia kunzei* (e.g., Felger & Zimmerman 2000, Pinkava 1999b, 2003b) to be *G. wrightiana* and the one previously called *G. parishii* in the flora area to be *G. kunzei*.

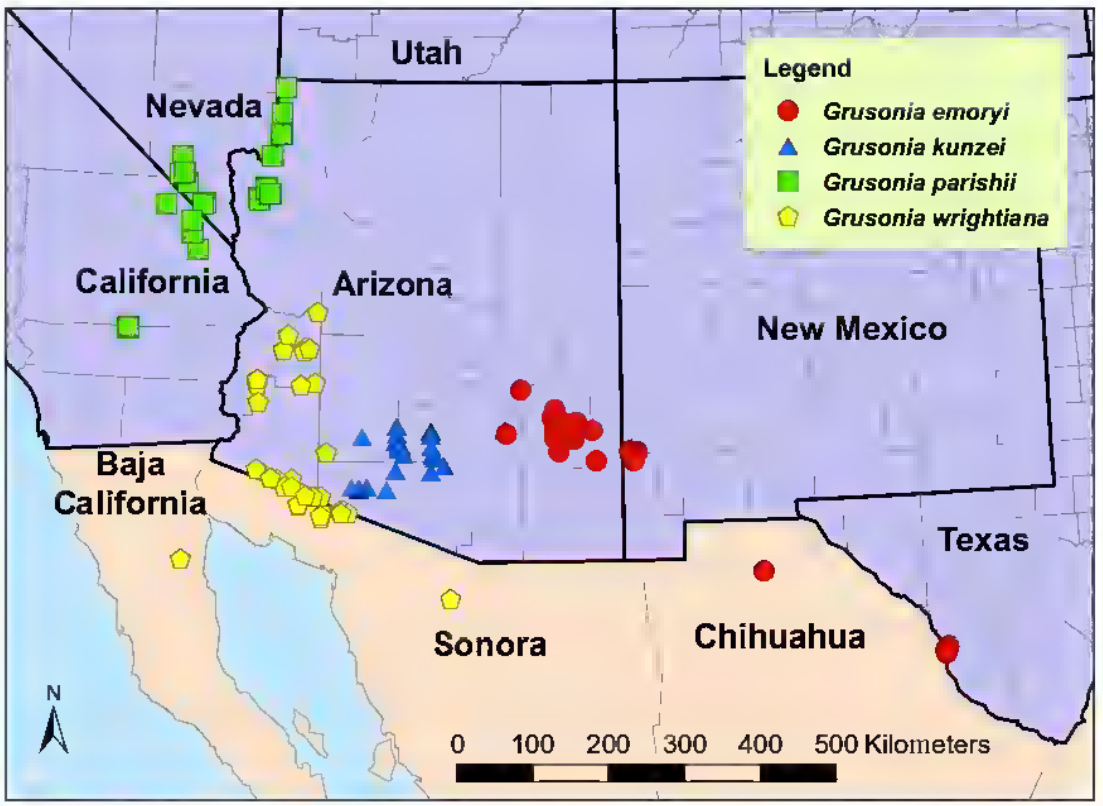

Figure 21. Specimen-based distribution of the four Arizona *Grusonia* species. Map by Marc Baker.

Some authors maintain that *Grusonia* and *Corynopuntia* are both valid and separate genera but, thus far, data supporting this viewpoint are inconclusive. Although *G. bradtiana* (J.M. Coulter) Britton & Rose, the type species for the genus, compared to other *Grusonia* is unusual with respect to some of its morphological and genetic attributes, it seems rather extreme to include *G. bradtiana* under its own monotypic genus.

Spine glands as extrafloral nectaries (EFNs) are documented for a number of *Grusonia* species. Michele Lanan (pers. com. to Felger, 21 May 2014) found that *G. emoryi* secretes tiny amounts of liquid from the ends of tiny developing spines on new growth, which is consistently collected by the dark rover ant (*Brachymyrmex patagonicus*) (figure 22), and once the spines grow larger they seem to stop secreting. Researchers have found EFNs on *Grusonia emoryi*, *G. invicta*, and *G. wrightiana* growing on the grounds of the Arizona-Sonora Desert Museum in Tucson (Marazzi et al., unpublished manuscript, and Joshua Ness, pers. com. to Felger, 21 May 2014). Marc Baker (6 Aug 2013) observed small black ants (probably *Brachymyrmex*) on the buds of *G. schottii* cultivated in Chino Valley, AZ. The ants were stroking the young spines with their various appendages. There was no reaction when Benedict's Reagent was applied to the areoles indicating the absence of simple sugars, while the same reagent applied to the areoles of young stems of *Cylindropuntia acanthocarpa* and *C. imbricata* stained the short hairs of the areoles orange-yellow. The ants on *G. schottii* may have simply been exploring or were obtaining nutrients other than simple sugars, or, as suggested by Michele Lanan (pers. com. to Felger, 21 May 2014), it might be that the ants were so efficient at removing the tiny amount of liquid that there was nothing left for the Benedict's reaction. Although "ants don't play" (Hölldobler & Wilson 1990: 370), biologists do.

1. Stems often 10–20 cm tall, formed of 1–3 joint(s); new branches arising from near ground level to over half way up stem; spines generally fewer than 15 per areole, the larger spines 2.2–4 cm long; fruits with glochids only. ..... **Grusonia kunzei**
1. Stems often 30–50 cm tall, formed of 2–6 joints; new branches held aloft and well above the ground; spines about 20 per areole, the larger spines 4–4.8 cm long; fruits with stout spines and glochids. ..... **Grusonia wrightiana**

Figure 22. *Grusonia emoryi*. Plant cultivated in Tucson, grown from a piece broken off by an off-roader at 32°47'25.66"N, 110°40'13.10"W, Route 77 north of Mammoth on a power line access road, Feb 2009, Pinal Co.: (A) nectar droplet on a spine-gland, (B) *Brachymyrmex* collecting nectar, photos by Michele Lanan, 21 May 2014.

Grusonia kunzei (Rose) Pinkava, J. Arizona-Nevada Acad. Sci. 32 (1): 50, 1999.
[*Opuntia kunzei* Rose, Smithsonian Misc. Collect. 50 (4): 505–506, 1908. *O. stanlyi* Engelmann ex B.D. Jackson var. *kunzei* (Rose) L.D. Benson, Proc. Calif. Acad. Sci., ser. 4, 25: 248, 1944. *Corynopuntia kunzei* (Rose) M.P. Griffith, Haseltonia 9: 91, (2003)].
Desert club cholla, devil cholla. Figure 23.

Low-growing club chollas often forming colonies 0.8–2 (5+) m across. Stem segments 1–3 per stem, clavate to elongate and tapering at both ends, erect, 5–13 cm long, generally 4–5 time longer than wide, with prominent tubercles 1.2–2.5 cm long. Spines very sharp, newly emerging spines pinkish, reddish, or reddish orange, becoming whitish to gray; the larger spines (upper centrals) mostly pointing downward, (2.2) 2.5–3.5 (5.8) cm long, and 1.2–1.8 mm wide and 0.5–1 mm thick at base. Flowers terminal, often several per stem, outer tepals yellow with salmon-pink midstripe extending into a long tooth, the inner tepals to about 2 cm long, pale yellow with some green at the base. Filaments greenish below and pale yellow above; anthers pale yellow. Fruits about 3.5–5 cm long, fleshy and yellow when ripe and usually soon becoming dry, with glochids but not spines; sometimes proliferating with a second fruit. Flowering in June and July, the flowers open in the late morning. Fruits ripening in late summer. $2n = 22$.

South-central Arizona in Arizona Upland of the Sonoran Desert, including the north-central and northeastern part of Organ Pipe. *Grusonia kunzei* in Organ Pipe occurs in localized but substantial colonies or assemblages of colonies on gravelly desert flats of gently sloping bajadas with sandy loams. Often growing with *Ambrosia dumosa*, *A. deltoidea*, *Carnegiea gigantea, Cylindropuntia acanthocarpa*, *C. fulgida*, *C. leptocaulis*, *Echinocereus engelmannii*, *Larrea divaricata*, *Mammillaria grahamii*, *Olneya tesota*, and *Parkinsonia microphylla*.

Grusonia kunzei most resembles *G. parishii* (Orcutt) Pinkava, which has wider upper central spines (to 3 mm), shorter tubercles, stem segments that are generally obovoid, and very low, trailing branches. *Grusonia parishii* occurs in the Mojave Desert in northwestern Arizona, California, and Nevada. Pinkava (1999b, 2003b) placed populations of what we now consider to be *G. kunzei* under *G. parishii* based on the low stature, $2n = 22$ chromosome number, and spineless fruits.

Although correctly classified by Benson in his first and second editions of *The Cacti of Arizona* (Benson 1940, 1950), he jumbled the taxonomy in his third edition (Benson 1969), which he carried over to his treatment of the cacti of the United States and Canada (Benson 1982). In these later works he erroneously placed populations of *Grusonia wrightiana* under the name *Opuntia stanlyi* var. *kunzei*, although the lectotype he chose had a spineless fruit (a feature of the actual *G. kunzei*, but not *G. wrightiana*). One factor that contributed to Benson's error was his confusion over the mileages given by Dr. R.E. Kunze for his locality data for his original (type) collection of *Opuntia kunzei*. Kunze stated in his correspondence to Rose that he found the plant 40 miles (the lectotype label, quoted below, has 26 miles) south of the Copper Mine (the present-day town of Ajo) and 25 to 35 miles north of the Mexican boundary. Benson (1982: 917) noted that, "the mileage figures do not check," probably with the assumption that Kunze went south from Ajo en route to the more recent border crossing at Lukeville. Kunze, however, stated that he traveled on the eastern slope of Gunsight Mountain Range (Gunsight Hills and Pozo Redondo Mountains), which indicates that he was along the well-established route at the time to Tucson via the Quijotoa Valley or possibly farther east (figure 21). Following this route, the mileages do check. In addition, Kunze said that "immense tracts between smaller arroyos were covered with this species." There are no such tracts of *Grusonia* between Ajo and Lukeville, but there are in the plains east of the Gunsight Hills. Pinkava (1999b, 2003b) followed Benson's error but was the first to note the problem of the spineless fruit on the lectotype, which he discovered after his treatments were published (Donald Pinkava, pers. comm. to Baker, 2012). Furthermore, we now know that the larger, lower-elevation and Lower Colorado

Valley species, *G. wrightiana*, does not occur east of the Gunsight Hills, east of Organ Pipe Cactus National Monument.

OP: Grass Canyon, NE corner of Monument, 17 Feb 1962, *Steenbergh 2-1761-1* (ORPI) 0.9 mi on Hwy 85 south of N boundary of Monument, gently sloping bajada, gravel and silt, *Cercidium microphyllum, Larrea* sp., *Ambrosia dumosa, A. deltoidea, Opuntia fulgida, O. acanthocarpa* var. *major, Echinocereus engelmannii, Mammillaria grahamii*, 22 Mar 1988, *Felger 88-110* (ARIZ, ASU). N boundary of monument, 0.2 km W of AZ Hwy 84, *Acourtia wrightii, Ambrosia deltoidea, A. dumosa, Bouteloua aristidoides, B. barbata, Carnegiea gigantea, Celtis pallida, Echinocereus engelmannii* var. *acicularis, Eragrostis ciliatensis, Ferocactus emoryi*

Figure 23. *Grusonia kunzei*. (A) Clonal colony, N boundary of Organ Pipe, W of Hwy 85, 10 Oct 2004. Hwy 85 near Armenta Ranch Road. (B) buprestid beetles, *Acmaeodera* sp., 31 Jul 2013, (C) 20 Oct 2013, (E) 31 Jul 2013, (F & G) plant and young, emerging spines, 31 Jul 2013. (D) N of Kuakatch Wash, E of Hwy 85, 13 Mar 2010

(rare), *Hilaria rigida, Krameria grayi, Larrea divaricata, Leptochloa filiformis, Mammillaria grahamii, Muhlenbergia porteri, Olneya tesota, Opuntia acanthocarpa, O. engelmannii var. leptocaulis, Peniocereus greggii* (rare), *Sporobolus cryptandrus,* 2 Dec 1990, *Felger 90-500* (ARIZ, ASU, DES). Vicinity of Walls Well, NE boundary of Monument, 19 Nov 2001, *Felger* (observation). 100 m SW of Hwy 85 and Armenta Ranch Road, *Rutman 31 Jul 2003.*

Pima County. "*Opuntia kunzei* Rose, sp. nov., twenty-six m. south of the Copper Mine, 04.603, 1904, *R.E. Kunze*" (lectotype of *Opuntia kunzei*, fruit on right side of sheet, US 535063 [Rose's type specimen of *Opuntia kunzei* includes Kunz collections from two different dates and two different places, therefore Lyman Benson (1982) chose the fruit on the right side of the herbarium sheet, with glochids but devoid of spines, as the lectotype.]).

Grusonia wrightiana (E.M. Baxter) E.M. Baxter, Calif. Cactus 58, 1935
[*Opuntia wrightiana* E.M. Baxter, Cactus & Succ. Jour. 4: 283, 1932 ("description meager but valid," Benson 1982: 917). *O. wrightiana* (E.M. Baxter) Peebles, Desert Pl. Life 9: 45, 1937. *O. stanlyi* Engelmann var. *wrightiana* L.D. Benson, Proc. Calif. Acad. Sci., ser. 4, 25: 248, 1944. *O. kunzei* var. *wrightiana* (E.M. Baxter) Peebles, Leafl. W. Bot. 5 (12): 192, 1949. *O. stanlyi* Engelmann var. *peeblesiana* L.D. Benson, Cacti Ariz. ed. 3, 20, 64, 1969. *Corynopuntia stanlyi* (Engelmann) Knuth var. *wrightiana* Backeberg, Cactaceae 1: 360, 1958]
Devil club cholla. Figure 24.

Cholla-like plants forming colonies often (0.5) 1–3.5 m wide. Branches often 30–57 cm tall, erect, stout, and tough, branching mostly from near base of plant, but with new branches held aloft and often branching from 6–10 cm above ground level. Stem segments 2–6 per stem, the larger stem segments 8.5–16 × 3.3–4.8 cm, more or less cylindroid with elongated, prominent tubercles. Spines stout, very sharp and rigid, about 20–30 per areole, most of the larger ones deflexed downward. Larger spines 4–5 cm × 1.5–2 mm maximum width, scabrous with minute transverse ridges, flattened or diamond-shaped in cross section; smaller spines terete; glochids few in upper part of areoles, or absent. Leaves to about 1 cm long, mostly red, and quickly deciduous.

Flowers 4.5–5.5 cm wide. Inner tepals pale yellow or cream colored, 25–3.5 cm long with a reddish central stripe; outer tepals pinkish, rather thick with thickened reddish tips, grading into the terete, reddish, and reduced pericarpel leaves. Filaments green basally, cream-white to yellow distally; anthers pale yellow. Stigma cream colored. Fertile fruits 4.5–8 × 2.4–3 cm, separating relatively easily from the stems, fleshy, obovoid, the pulp yellowish, the skin dull yellow, the areoles with spine clusters and glochids; floral remnants persistent. Sterile fruits often present, with floral remnants but without seeds, usually cylindroid (more narrowly cylindroid than the fertile fruits), remaining green, and more firmly attached to the stems than the seed-bearing fruits. Seeds 3.3–5 mm long, light tan, smooth. Flowering April, May and June; ripe fruits seen from late August until the following May. As the fleshy, yellow fruits ripen, almost all of them (at least during dry years) are chewed open on one side, presumably by small mammals and/or perhaps by birds and the seeds removed.

Common in the Lower Colorado Valley region of the flora area, on sandy flats along the southwestern margin of Organ Pipe and across much of Cabeza Prieta on valley flats and low hills; sandy or silty soils, often with *Larrea* on low sand hummocks (the hummocks seem to form as a result of sand trapped by the cactus colony) and less often on pavements and rocky slopes. Especially abundant on sand flats and low, stabilized dunes in the south-central and southwestern part of Cabeza Prieta and occasional in the Lechuguilla Valley east of Tinajas Altas.

Northwestern Sonora from the Pinacate Region southward near the coast to Bahía San Jorge (vicinity of 31° 10' N) and eastward to Tubutama (vicinity of 30° 53' N, 111° 27' W), northeastern Baja California in the San Felipe Desert, and southwestern Arizona in western Pima County, and

Yuma and La Paz Counties (figure 21). Lyman Benson (1982: 365) tells that this club cholla "in California was reported by Baxter (1932, 1935), and the report was accepted by Wiggins (1963) . . . [and although it] . . . does occur just east of the Colorado River in Yuma Co., Arizona, no specimens from across the river in California have been seen." Marc Baker and Michelle Cloud-Hughes searched for it on several occasions in potential habitat in California but did not find it there

OP. Quitobaquito, Jan 1894, *Mearns 2735* (CAS). Quitobaquito, 27 Nov 1939, *Harbison 26175*. Quitobaquito, 5 Mar 1940, *Peebles 14561*. 6 mi E of Quitobaquito [based on data from Lehto's notebooks], 24 Oct 1965, *Lehto 5489-b* (ASU). 1 mi NW of Border Monument 180, T15S, R12W, 700 ft, low sand dunes, 10 Apr 1978, *Lehto L-22481* (ASU). 0.9 mi E of Aguajita Spring, *Atriplex polycarpa*, *Ambrosia dumosa*, *Suaeda*

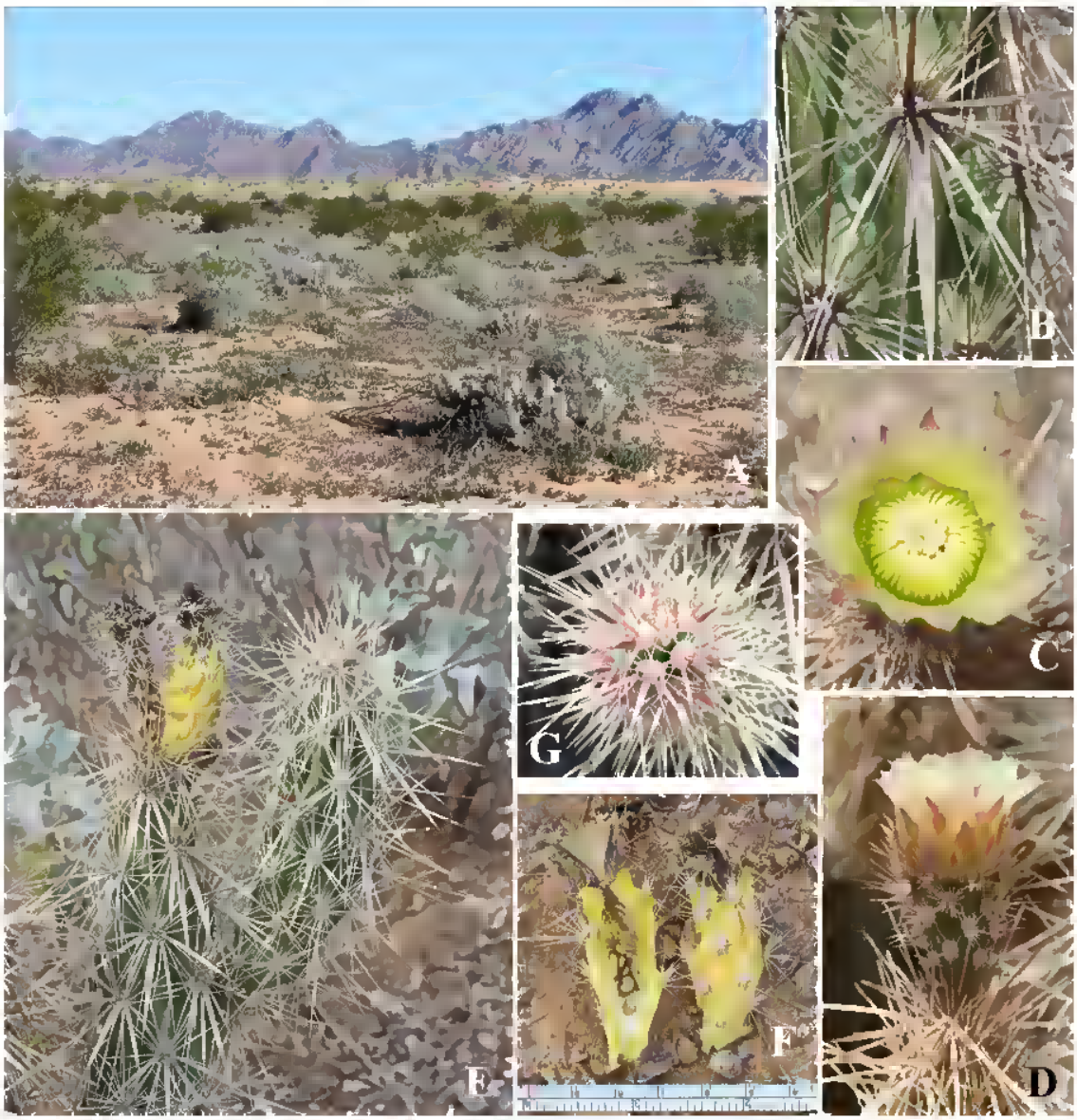

Figure 24. *Grusonia wrightiana*. (A) Pinta Sands, 11 Feb 2014. La Abra Plain at U.S./Mexico boundary. (B) Sonora, 26 Aug 2013; (C & D) Organ Pipe, 22 Jun 2006; (G) young, emerging spines, Sonora, 26 Aug 2013. (E & F) Garden in Why, 4 Jan 2014.

moquinii, *Larrea*, *Echinocereus engelmannii*, *Ferocactus emoryi*, 6 Apr 1988, *Felger 88-324* (ASU). 0.9 mi W of Quitobaquito (at old fields below pond) on border road, sandy-gravelly soil of low hills and flats, *Atriplex polycarpa*, *Carnegiea gigantea*, *Fouquieria splendens*, *Olneya tesota*, *Opuntia acanthocarpa*, *Ambrosia dumosa*, *Mammillaria thornberi*, *Proboscidea altheifolia*, 14 Sep 1988, *Felger 88-469*. Aguajita Wash, very fine loam, *Atriplex polycarpa* flat, *Atriplex polycarpa*, *A. linearis*, *Atamisquea*, *Larrea*, *Prosopis*, *Lycium*, 13 May 1988, *n* = 22, *Baker 7613* (ASU). 0.4 mi E of Aguajita Wash along Puerto Blanco Drive, sandy flat with *Atriplex polycarpa*, *Larrea*, 19 Jun 1989, *Felger 89-231*. Hocker Well, 3 Dec 1990, *Felger* (observation).

CP: Papago Wells, 1 Mar 1939, *Nichol 1 Mar 1939*. 1 mi NW of Border Monument #180, 700 ft, low dunes, 10 Apr 1978, *Lehto L-22481* (ASU). Tule Well, sandy flat and wash, saline soil, 6 Apr 1979, *Lehto L-23567* (ASU). Between Half Way Tank and Buck Peak Tank, 14 Jun 1992, *Felger 92-607*. 1.7 mi on Camino del Diablo E of W border of Refuge, 16 Jun 1992, *Felger* (observation). 7 mi W of O'Neill's grave, sand flats including *Larrea*, *Hilaria rigida*, few *Camegiea*, *Echinocereus engelmannii*, few *Ferocactus wislizeni*, 15 Sep 1992, *Felger 92-784*. 24.5 mi SW of Cabeza Prieta boundary with Organ Pipe, Camino del Diablo en route to Pinta Sands, 32°05'N, 113°28'W, sandy soil, with *Opuntia ramosissima*, *Echinocereus engelmannii*, *Ferocactus* sp., *Carnegiea*, etc., 4 Mar 1995, *Rebman 2880* (ASU, DES, UCR). Just W of Pinacate Lava Flow, *Larrea tridentata*, *Ambrosia dumosa*, 7 Apr 2002, *Hodgson 18704* (DES).

TA: Tinajas Altas, 9 Mar 1937, *Harbison 16999 & 17000* (SD). Camino del Diablo, E of Raven Butte, 29 Nov 2001, *Felger* (observation).

Yuma County: Petrified Forest near Colorado River, 4 mi W of Quartzsite-Yuma road, 33 mi N of Yuma, *Allan B. Clayton 15 Apr 1934* (holotype of *Grusonia wrightiana*, DS 691434 [CAS]).

Lophocereus

This genus includes three species. *Lophocereus gatesii* M.E. Jones occurs in southern Baja California Sur and *Lophocereus marginatus* (de Candolle) S. Arias & Terrazas (*Pachycereus marginatus* (de Candolle) Britton & Rose) occurs in south-central Mexico (Arias & Terrazas 2009).

Lophocereus schottii (Engelmann) Britton & Rose var. schottii

[*Cereus schottii* Engelmann. *Pachycereus schottii* (Engelmann) D.R. Hunt]
Senita; *sinita*, *misaro*; cei:m i. Figure 25.

Many-stemmed columnar cacti, often 2–4 (7) m tall branching mostly at or near the base of the plant, often forming clonal colonies (Parker 1989). Stem tissue becoming black on cut surfaces (also see *Carnegiea* and *Cylindropuntia fulgida*). Stems strongly dimorphic—as the stems elongate, usually after reaching more than about 1.5 m in height, they become more slender, much less fleshy, and the number of stem ribs increases. Lower portion of stems, sterile (not producing flowers), with 5 stem ribs, relatively thick, the larger stems often (8.5) 14–16 cm diameter, the areoles widely spaced and the spines often 5–7 mm long, stout and rigid, not markedly twisted, and with enlarged bases. Upper part of the stems fertile (producing flowers), with 5–7 stem ribs, relatively slender, often 5.5–10 cm diameter, the areoles close together to essentially contiguous, and bearing a dense, shaggy covering of long, slender, twisted, and often flattened spines 4–10 cm long, these spines obscuring the stem surface.

Fertile areoles multiple-flowered (*Myrtillocactus* of Mexico is one of the few other genera of cactus producing more than 1 flower per areole). Flowers nocturnal, 2.5–4 × 3.8–4.2+ cm; weakly bilaterally symmetrical (the tube slightly curved upward, the style lying near the lower side of the tube). Inner tepals whitish to pinkish, spreading open early in the evening (e.g., 8 p.m. on a hot, mid-August night) and becoming recurved before sunrise. The flowers open shortly after sunset and close before or soon after dawn, although the flowers stay open longer in cooler weather, and on cool spring days they may remain open nearly all day. (In Sonora, Richard found that flowers open when a flowering stem is taken from midday summer heat to an air-conditioned room). Filaments, style, and stigmas white, the anthers cream colored. Flowering and fruiting mostly through the hotter months: flowers recorded March–December, but mostly April–September; fruits April–December, peak fruiting often in June. Fruits ovoid to globose, 2–4 cm diameter, essentially spineless, becoming

bright red and edible when ripe, irregularly splitting from the top, the pulp bright red; seeds small and blackish. At peak fruiting during favorable years, the upper stems often are loaded with bright red fruits. The pulp and seeds avidly consumed by birds and carried away by ants, and it is often difficult to find ripe fruits in the morning before the birds and ants have hollowed them out. Seeds blackish (dark red-brown under magnification and strong light), (2.2) 2.4–2.8 × 1.8–2.1 mm, shiny and smooth, with a low ridge.

Locally along the southern border of Organ Pipe, westward from the Santa Rosa Mountains, and most common in Senita Hills and the granitic outwash plain of the Senita Hills in the La Abra Plain (Parker 1989). A spectacular stand of organ pipes, saguaros, and senitas occurs in Lost Cabin Basin near Victoria Mine. Also at a few localities, and rare, in the southern part of Cabeza Prieta. Senitas are more common in nearby areas in Sonora. Their distribution in Arizona and northern Sonora is limited by freezing weather, and presumably the western distribution in northwestern Sonora and western Arizona is limited by drought (e.g., Turner et al. 1995). "Evidence of freeze damage, indicated by callused stem tips with new stems emerging from just below the callus tissue or elsewhere on plants, is widespread among senita populations in Arizona and [nearby] northern Sonora (Felger and Lowe, 1967; Nobel, 1980)" (Parker 1989: 399; similar freeze-damage also is evident on organ pipe plants, *Stenocereus thurberi*). During the extreme drought of the 2000s, widespread and significant mortality of senitas occurred in parts of northwestern Sonora and to a lesser extent in Organ Pipe.

Variety *schottii* is characterized by relatively thick stems, 5–8 stem ribs, and an essentially trunkless, or basitonic, branching habit. This is the northern variety, restricted to the Sonoran Desert in southwestern Arizona and western Sonora, Baja California, and Baja California Sur northward from La Paz. It ranges southward in Sonora to the Guaymas region. Two individual senitas were found in the Chuckwalla Mountains of southeastern California that appear to be wild but are only 0.5 km from what was once a private residence. One of the individuals flowers but does not form fruits, indicating that the species is an obligate outcrosser and that there are no other mature individuals within pollination distance. This is the only population of this cactus in the United States apart from southwestern Arizona (Cloud-Hughes & Baker, accepted for publication).

Variety *schottii* in Sonora is replaced to the south by var. *australis* (K. Brandegee) Borg (var. *tenuis* G.E. Lindsay), which ranges southward from the coastal plains southeast of Guaymas (vicinity of Potam) into northwestern Sinaloa (vicinity of Guasave). A similar scenario occurs in southern Baja California Sur. Variety *australis*, primarily in thornscrub, has relatively slender stems with 6–10 ribs, branches arise at various heights well above the base, and the plants often form short trunks (especially towards the Sinaloan border). Although Lindsay (1963) named the southwestern Sonora plants var. *tenuis*, they appear morphologically indistinguishable from var. *australis*, described by Brandegee (1900) from the Cape Region of Baja California Sur (Felger & Wilder 2012).

In *Lophocereus schottii* there is a great variation in stem size ranging from larger stems with fewer stem ribs (5–7) in the northern Sonoran Desert to smaller and more slender stems with 6–10 ribs in thornscrub in southern Sonora (figure 35 c & d; also see *Peniocereus striatus*). The clinal shift in architecture and morphology, from stems with a higher surface-to-volume ratio in the south to stems with a lower surface-to-volume ratio in the north, is interpreted as an adaptation to increased aridity northward (Felger & Lowe 1967; also see Turner et al. 1995).

Patrolling ants attracted to extra-floral nectaries in the areoles provide protection from herbivorous insects (Turner et al. 1995). "Developing buds, flowers and immature fruits produce extrafloral nectar (EFN) from the tips of tepals, photographs of which can be found in Chamberlain & Holland (2008). In addition to reproductive tissues, *P. schottii* has extrafloral nectaries just below their areoles (sub-areole nectaries), but secretion from them has been largely observed after flowering

seasons on new stem growth" (Holland et al. 2009: 90–91). Much like the well-known mutualism between yuccas and yucca moths, there is an obligate relationship between sinita and a pyralid moth, *Upiga virescens* (e.g., Fleming & Holland 1998, Hartman et al. 2002). The female moths collect pollen on specialized abdominal scales and actively deposit pollen on the stigma, and deposit a single egg in each pollinated flower. The larvae feed on sinita ovules, preventing seed set in individual fruits, but enough flowers escape predation to produce significant numbers of fruits and seeds. However, seedling establishment among the northern populations is a rare event and clonal propagation from stems is a more common occurrence.

Figure 25. *Lophocereus schottii*. Senita Basin: (A) 14 Jan 2014; (B) 18 Jun 2012. (C) La Abra Plain, Organ Pipe, 22 Jun 2006. Organ Pipe headquarters: (D) 18 May 2006; (F) 22 May 2006. (E) Immature, or sterile stem tip, Sierra Blanca, Pinacate Biosphere Reserve, 18 Jan 2009.

The name "senita," in common use in Arizona, is a corruption of the Mexican vernacular name "sinita." The fruits are edible but not as sweet and not nearly as large as organ pipe and saguaro fruits (e.g., Betty Melvin in Zepeda 1985: 55). The stems are highly esteemed in Mexico for medicinal purposes, especially stems with five ribs. Considerable quantities are harvested for personal and commercial purposes (e.g., Felger 2000, 2007; Paredes et al. 2000). Five-ribbed stems are the sterile or juvenile growth, and are thicker, "softer" (more flaccid and much juicier), and not as tough as fertile parts of the stem with a higher number of ribs. The 5-ribbed stems are used in remedies for diabetes, stomach ulcers, and cancer, and also as a remedy for falling hair (*evita la caida pelo*) and blood circulation (*circulación de la sangre*). As a common preparation, a cross section of the stem, about 2 cm thick, is cooked in about one liter of water until it boils. This liquid is then drunk through the day as one would drink water (*se pone en un litro de agua hasta hervir, y se toma como agua de diario*). The fresh as well as dried star-shaped cross-sections of stems are widely sold in herbal shops in Mexico, even as far as Mexico City and Tijuana. *Músaro*, derived from the Yoeme (Yaqui) language, is the name often used in Mexico.

OP: Gray's Well [= Blankenship Well at Dos Lomitas], *Nichol 4 May 1939* (ORPI). 1 mi E of Quitobaquito, S slope, gravelly silt, few, 2 Jun 1951, *Blakely 323* (DES). 2.4 mi W of Hwy 85 on Puerto Blanco Drive, 19 Jun 1989, *Felger 89-229*. Dos Lomitas, 13 May 1990, *n* = 11, cited in Madroño 39: 106, 1992 [Pinkava et al. 1992b], *Baker 7831-A* (ASU, ORPI). 1 mi W of Lukeville at international boundary, 18 Nov 1991, *Felger* (observation).

CP: 7 mi E of Papago Well, 14 Mar 1937, *Harbison 17061* (SD). Davidson Canyon (Simmons 1965: photo, 2 Feb 1964). SW side of Agua Dulce Mts, 32°02'N, 113°18'W, sandy flats, about one dozen plants to 7 ft tall, 12 May 1997, *Luke Evans* (observation).

Sonora: Sierra de Sonoyta, and southeast towards Santa Magdalena, *Schott July 1855* (holotype, MO, the protologue says "Sonora, towards Santa Magdalena").

Mammillaria – Fishhook cactus; *cabeza de viejo*

The three species in the flora area are small cacti of unrelated species in this large genus. Stems globose to cylindroid with distinct (separate) tubercles. Tubercles each with a terminal spine-bearing areole and subtending a very reduced, axillary, flower-bearing areole that sometimes also bears a few bristle-like spines. Central spines hooked (those in the flora area). Flowers diurnal and relatively small for the family. Fruits succulent, globose to elongated, smooth (spineless), red. All three of species in the flora area are $2n = 22$. During the decade preceding 2014, *Mammillaria* plants in the flora area have been dying due to drought and drought-related responses such as increased herbivory.

The genus includes 165 species, mostly in Mexico, some in southwestern USA, and few in the West Indies and Central America.

1. Seeds 1.6–2.4 mm long, the lower ⅓ covered with a light-colored, corky cup-like base, the seed surface reticulate and wrinkled but not pitted (note: dried fruits can often be found below the spine clusters in the tubercle axils); fruits not good to eat. ..... **Mammillaria tetrancistra**
1. Seeds slightly less than 1 mm long, without a corky base, the seed surface pitted; fruits good-eating.

2. Hook of central spine 2–3 mm across; stems commonly 3.5–6 cm wide; stigma green; widespread across the flora area, rocky places and plains..... **Mammillaria grahamii**
2. Hook of central spine 1.5 (2) mm across; stems commonly (2) 3–3.5 cm wide; stigma magenta; lower bajadas and desert flats in Organ Pipe. ..... **Mammillaria thornberi**

Mammillaria grahamii Engelmann

[Among the many synonyms are: *M. grahamii* var. *arizonica* Quehl. *M. grahamii* var. *oliviae* (Orcutt) L.D. Benson. *M. microcarpa* (Engelmann) Britton & Rose. *M. milleri* (Britton & Rose)

Bödeker. *M. sheldonii* (Britton & Rose) Bödeker. *M. swinglei* (Britton & Rose) Bödeker]
Arizona fishhook cactus; *cabeza de viejo*; ban 'isvig, ban cekida. Figure 26 A–C.

Stems single (unbranched) or with 1 to several branches; stems globose to cylindroid, 5–15 (30) × 3.5–6.5 cm. Central spines 1–3 per areole, at least 1 of them strongly hooked. Flowers often 2–3.5 cm wide, usually in a ring near the top of the stem. Inner tepals showy, pink to rose purple. Stigma green. Fruits edible. Seeds 0.75–0.95 mm diameter, rounded-obovoid, blackish, and pitted. In southern Arizona several flushes of flowers may be produced annually, each about 5 days after soaking rains (Bowers 2002).

Widespread and common across the flora region including sandy and rocky soils of valley plains, bajadas, and rocky slopes to higher elevations. Plants in granitic mountains tend to have pale spines whereas those in volcanic areas tend to have dark spines. A fishhook cactus resembling this species has been in the flora area for more than 20,000 years. *Mammillaria grahamii* occurs with *M. tetrancistra*, and with *M. thornberi* from Quitobaquito to the nearby Río Sonoyta in Sonora and in the lower Sonoyta Valley in Organ Pipe. Seeds of *M. grahamii* and *M. thornberi* appear to be indistinguishable.

As broadly interpreted, *M. grahamii* ranges from southeastern California to west Texas, northern and western Chihuahua and most of Sonora nearly to the Sinaloa border. Distinguishing varieties or subspecies is problematic. *Mammillaria grahamii* subsp. *sheldonii* (Britton & Rose) D.R. Hunt [*M. swinglei* (Britton & Rose) Bödeker] occurs in coastal Sonora from about Puerto Libertad to the southwestern part of the state. Subspecies *sheldonii* is reported to have smaller and whitish flowers and fewer radial spines (12–15) than subsp. *grahamii* (20–30+), but other than flower color, consistent distinguishing features appear elusive (Felger & Wilder 2012).

Fresh fruits of this species and the less common *M. thornberi* are tasty and were eaten by children and probably by people of all ages as trail snacks (Felger & Moser 1985; Hodgson 2001). Ear drops prepared from the stems served as a treatment for earache for Gila River Pimas and Seris (Curtin 1949; Felger & Moser 1985). Gila River Pimas rubbed the red fruits "on arrowshafts to color them" (Curtin 1949: 57).

OP. Cipriano Well, *Nichol 27 Apr 1939* (ORPI). Bates Well, 5 Mar 1940, *Benson 9945*. Quitobaquito, 29 Mar 1988, *Felger 88-129*. Trail from The Cones to Mount Ajo, 4100 ft, 10 Apr 2005, *Felger* (observation) †*M* cf. *grahamii*. Alamo Canyon, spines, seeds, 1150 to 14,500 ybp (3 samples). †Montezuma's Head, spines, seeds, 20,490 & 21,840 ybp †Puerto Blanco Mts, on ridge, spines, seeds, 990 to 7580 ybp (8 samples).

CP. Observations. Sand over lava at E side Pinacate flow, 31 Jan 1992, *Felger*; Senita Tank, 14 Jun 1992, *Felger*.

TA. Granite mountain at NW side of Raven Butte, 30 Dec 2005, *Felger 05-384*. 0.3 mi SE of Tinajas Altas, upper bajada, decomposed granitic rocky soil, 1175 ft, 22 Nov 2008, *Felger 08-193* (DES). †M. cf. grahamii, Tinajas Altas, spines, seeds, 1230 to 18,700 ybp (11 samples).

Mammillaria tetrancistra Engelmann
Corkseed fishhook cactus; *cabeza de viejo*. Figure 26 D–G.

Stems single (unbranched) or with 1 to several branches, areal part of stems globose to cylindroid, and often 5–10 × 3.5–6 cm; underground portion of stem usually thickened, flabby, root-like, often 5–8 cm long; upper part of roots also often thickened. Spines dark or light colored depending largely on substrate color (see *Ferocactus cylindraceus* and *Mammillaria grahamii*); central spines hooked, 1–3 (4) per areole. Flowers 2.5–3.5 cm wide, pink, spring and summer, and not arranged in a ring (as in *M. grahamii*). Outermost tepals with relatively long-fringed margins (use hand lens; figure 26-E). Inner tepals pink-magenta, often with paler-colored margins. Stigma yellow

or yellow-green. Fruits succulent, bright red and longer than wide. Seeds (not including strophiole) 1.6–2.4 mm at widest point, the surface rugose-roughened over a reticulate cellular pattern and not pitted; basal 1/3 of seed covered with a light-colored, corky aril-like cup (the *strophiole,* a specialized outgrowth or proliferation of hilum tissue), the strophiole pale colored and spongy when fresh, drying brown and corky and remaining firmly attached to the seed. Although the fleshy part of the fruit is edible, the seed cork will make you spit it out—an easy way to identify this species.

Rocky soils, hills and mountains, and sometimes adjacent middle to upper bajadas, from the Tinajas Altas Mountains across Cabeza Prieta, and lower elevations in Organ Pipe. Often growing intermixed with *M. grahamii*.

Western Arizona, southeastern California, southern Nevada, southwestern Utah, northwestern Sonora, and northeastern Baja California.

Figure 26. *Mammillaria grahamii*. (A & B) SW of Hwy 85 & Armenta Ranch Road, Organ Pipe, 30 Jul 2013, (C) Ajo, 6 Sep 2013. *Mammillaria tetrancistra*. (D & E) flower and tepal margin, El Huerfano, Sonora, 5 Sep 2013, (F & G) N of Dos Lomitas, Sonoyta Valley, Organ Pipe, 23 Aug 2012. *Mammillaria thornberi*. (H & I) W of Quitobaquito, 13 Sep 2006, (J) near El Huerfano, Sonora, 26 Aug 2013.

The plants are deceptively similar to *M. grahamii* when not in flower although they are not closely related within the genus. Apart from the distinctive seeds and flowers, *M. tetrancistra* may be identified by its relatively smooth, soft, extensive, and deeply buried stem-base (often wedged between rocks); surprisingly soft-skinned and flaccid stems and tubercles (not firm like those of *M. grahamii*); mucilaginous pith and cortex (tangible even on the smallest cut surfaces, such as tubercle sections); radial and subcentral spines that do not radiate as neatly and regularly as those of *M. grahamii*, giving the plant a relatively shaggy appearance or a "salt-and-pepper" color-pattern rather than a "well-groomed" appearance; and narrower and more numerous tepals, the outer tepals with relatively large fringes. The seeds of *M. tetrancistra*, with their corky base, are unlike those of any other cactus. It is the most arid-inhabiting of all mammillarias.

OP: 0.5 mi N of Mexican Border, 3 mi E of Lukeville, 6 Jan 1962, *Steenbergh 1-662-1* (ORPI). Growler Mine, Bates Mts, 13 Sep 2013, *Rutman*, photos.

CP: Near Tule Mts, 4 mi E of Tule Well, 29 Feb 1976, *McManus 688*. T15S, R12W, S18, lava flow, 7 Apr 1979, *Lehto L23574* (ASU). Childs Mt, 2240 ft, 9 Apr 1993, *Felger 93-303*. Growler Mountains, S of Charlie Bell Pass, 9 Apr 1993, *Felger* (observation).

TA: Granite hills at SW side of Tinajas Altas Mts, 10 Jan 2002, *Felger 02-6*. Camino del Diablo SSE of Raven Butte, 20 Feb 2005, *Felger* (observation).

Mammillaria thornberi Orcutt
[*M. fasciculata* of authors, not Engelmann]
Thornber fishhook cactus; *cabeza de viejo*; ban mauppa. Figure 26 H–J.

Stems often (2) 3–3.5 cm diameter, more than twice as long as wide, usually somewhat flaccid, branching from the base and along the stem to eventually form spreading, many-stemmed plants, these sometimes breaking apart, the pieces forming adventitious roots, or the plants occasionally with only a few branches. Hooked central spines 1 per areole. Inner tepals white or pale pink with a bright rose-pink midstripe. (The inner tepals are broader than those of the two other mammillarias in the region). Filaments rose-pink; anthers yellow. Stigma magenta. Seeds 0.9 mm diameter, similar to those of *M. grahamii*. Flowering July and August.

Locally common along the southern margin of Organ Pipe and also in the northwestern part of the Monument. Sandy to gravelly soils of lower bajadas and desert flats, usually under small shrubs, especially *Ambrosia deltoidea*, *A. dumosa*, *Atriplex linearis*, *A. polycarpa* and sometimes among fallen joints of *Cylindropuntia fulgida*, and rarely under *Suaeda nigra*. Highest density is in saltbush vegetation on Holocene-aged surfaces. Often growing intermixed with *M. grahamii*.

Southwestern Arizona and northwestern Sonora southward to sandy plains southwest of Caborca.

Mammillaria thornberi is closely related to, but obviously distinct from, *M. yaquensis* R.T. Craig, which occurs on fine-textured, alluvial soils of the coastal plains of Sonora from near Empalme and Las Guásimas (southeast of Guaymas) southward to northwestern Sinaloa. The two species are disjunct by several hundred kilometers. *Mammillaria yaquensis* differs in part by its markedly more delicate and slender stems and more profusely branching habit, the branches often arise well above the lower part of the stem, and smaller and more readily detaching branches. There is no indication of plants with intermediate features.

OP: Quitobaquito, 28 Nov 1939, *Harbison 26183* (SD). 10 mi E of Hwy 85 on Mexican Boundary, 26 Jan 1962, *Steenbergh 1-2662-1* (ORPI). Hocker Well, 3 Dec 1990, *Felger 90-575*. 0.5 mi W of Growler Wash on Bates Well Rd, loamy flat, under *Larrea*, *Rutman 23 Aug 2001* (ORPI).

†**Mammillaria** sp.
TA †Butler Mts, hooked spines, 740 & 3820 ybp

Opuntia – Prickly-pear; *nopal*

Stem segments, or pads (cladodes), laterally compressed. Areoles bearing glochids and with or without spines. Areoles of young developing pads and flowers (fruits) bearing extrafloral nectaries and a small, green, succulent, conical, and soon-deciduous leaf. Flowers relatively large, diurnal, with sensitive stamens (filaments closing inward when touched). Fruits fleshy or dry. "Seeds" relatively large, the actual seed covered with a white to light tan bony aril-like structure (see *Cylindropuntia*).

The genus includes about 150 species, native from Canada to South America.

1. Pads 9–12.5 cm long, generally bluish to purplish, minutely hairy (use 10× lens); areoles with glochids but spines lacking; inner tepals rose-pink. ..... **Opuntia basilaris**
1. Pads usually 15 cm long or more, glabrous, green or sometimes reddish purple; areoles with glochids, and at least some areoles with spines; inner tepals yellow to pale orange (tepal bases reddish in *O. phaeacantha*).

2. Plants erect, often with a short but well-developed trunk; pads more or less orbicular; spines yellowish, becoming blackish with age, mostly pointing downward. ..... **Opuntia chlorotica**
2. Plants often sprawling-spreading, trunk not well developed; pads obovate to elliptic; spines mostly white with brownish bases or if yellow then relatively robust and the largest one porrect and/or spreading (pointing in different directions).

3. Flowers uniformly yellow when first open, becoming pale orange with age but of a single color; fruits very juicy, the pulp and skin rich red-purple..... **Opuntia engelmannii**
3. Flowers yellow with a conspicuous reddish center; fruits only moderately juicy, the skin pinkish to reddish, the pulp whitish or greenish, not bright purple..... **Opuntia phaeacantha**

Opuntia basilaris Engelmann & J.M. Bigelow var. **basilaris**
Beavertail cactus. Figure 27.

Dwarf prickly-pears, often 25–50 cm wide, forming a very thick, short caudex giving rise directly to thick, stubby pads that sometimes curl inward. Individual stems of 1 or rarely 2 pads (cladodes). Pads 8–14 × 4–10 cm (reaching 18 cm long in cultivation), the surfaces minutely and densely puberulent (use 10× lens), pale bluish (the color does not rub off), somewhat pale purplish during cooler, drier months. Areoles bearing dense tufts of glochids, which are barbed, but no spines. Young areoles on developing pads have transparent tubular hairs and minute, cone-shaped red leaves, which are pubescent with minute, short, thick hairs; leaves soon deciduous. (Marc Baker observed small black ants apparently feeding on surface compounds of the tubular hairs of the areole and of the small hairs on the leaves of a plant from the type locality of *O. basilaris*. A test with Benedict's Reagent, however, did not detect simple sugars). Flowers 7–7.5 cm wide, showy, opening for 1 or 2 days; outer tepals thick and fleshy, greenish brown, the inner tepals bright rose pink, 4–4.5 cm long, the larger tepals 2.5–3 cm wide. Filaments red; anthers pale yellow: the showy stamens with red filaments and yellow anthers are noteworthy. Style pale rose pink, darker on the second day; stigmas pale yellow, opening on the second day. Fruits dry at maturity. "Seeds" 7–9 mm wide, puffy, looking like compressed garbanzo beans. Flowering in early April, the fruits ripening in late May; $2n = 22$, 33 (M. Baker, unpublished data).

Arid, western margin of the flora area: southwestern corner of Cabeza Prieta and the Tinajas Altas Mountains. On nearly barren desert pavements, canyons and rocky slopes, and also granitic mountains in adjacent Sonora west of the Pinacate lava (Felger & Zimmerman 2000). No other prickly-pear extends into such hyperarid regions. This small prickly-pear ranges from the pediment

base to nearly the summit in the Tinajas Altas Mountains; at higher elevations it occurs in localized soil pockets. Its history in the Tinajas Altas region extends to more than 37,000 years.

Many pads have a dead, dried area below the old flower or fruit—the pad tips desiccate. In drought conditions the pads shrivel and wrinkle, and some or even most or sometimes all of the pads drop off in severe drought like deciduous leaves. Thus, in the most severe drought conditions the thick, succulent caudex functions like a thick, tuberous root. The pads are relatively dwarfed in comparison with those of the same variety of beavertail cactus from other regions, but in cultivation (in Tucson) the pads of plants from the flora area can become substantially larger than ones seen in the wild.

Western Arizona, northwestern Sonora, southern California, southern Nevada, southwestern Utah, and northern Baja California. Several varieties are recognized; variety *basilaris* nearly encompasses the distribution of the entire species. In 2014 Rutman observed beavertail plants volunteering in some Ajo neighborhoods, presumably from seeds dispersed by birds from cultivated plants.

Richard writes: "I remember my first cactus collection. My family had gone to Palm Springs, California, for a vacation. I was five or six years old and fascinated by a beavertail cactus and put a pad in my pocket. Much later I learned that the highly irritating glochids can be removed with adhesive tape or shaving the afflicted surface (the glochids eventually dissolve)." Bean and Saubel (1972: 95) report that the Cahuillas in California ate the fresh fruits and that the flower buds were pit-baked or sometimes dried and stored, the pads boiled as a vegetable, and the "seeds ground into an edible mush." This is one of few references to *Opuntia* "seeds" being eaten. The fruits hardly seem worth eating "fresh" since they are dry at maturity, or maybe they were harvested just before becoming dry?

CP. E edge of Lechuguilla Desert (Simmons 1965, 1966). Bajada of Tordillo Butte, 4 mi on Camino del Diablo E of the W border of the Refuge, basalt-sand flat outflow from Tordillo Butte to the NE, 16 Jun 1992, *Felger 92-621*

TA. Observations, *Felger*: Borrego Canyon, 3 Feb 1990, Tinajas Altas, 29 Nov 2001. Tinajas Altas Pass, 32.31444°N, 114 08556°W, 329 m, rocky granitic slope and derived gruss, 2 Mar 2014, *Susan Davis Carnahan*, 2 photos (MABA in SEINet). Variety unknown: †Tinajas Altas, seeds, 1230 to 11,040 (8 samples), & >37,000 ybp.

Opuntia chlorotica Engelmann & J.M. Bigelow
Pancake prickly-pear; *nopal rastrero*. Figure 28.

Shrub-sized prickly-pears, often 1–1.6 m tall, developing a short, stout trunk. Pads (10) 13–23 × (10) 13–25 cm, erect, oval, obovate, or nearly round in outline, moderately glaucous, not becoming reddish or purplish. Areoles all bearing spines, or a few lowermost areoles without spines. Spines straw colored, mostly pointing downward; persisting on older pads and trunk and becoming grayish or blackish, those of lower areoles often long and shaggy. Flowers large, inner tepals yellow with a faint red midstripe even when freshly open; stigmas green. Fruits fleshy, glaucous, rose pink. Flowering in April. $2n = 22$.

Middle to higher elevations in mountains, especially in the northern and eastern part of the flora area; absent from lowland flats. Rare, single plants, however, occur where it is not expected, e.g., Sue Rutman found one plant in the 1990s at the base of the Pozo Nuevo Hills and another one in 2013 in Acuña Valley.

Unlike most other cacti in the region, this species seems to have expanded its range in the wetter rainfall climates of the Wisconsin glacial environments, a time of greater winter rainfall and drastically reduced summer rains. It is documented in Organ Pipe for 32,000 years, and more than

11,000 years in Tinajas Altas where it no longer occurs.

Arizona, northern Sonora, Baja California, northwestern Chihuahua, southeastern California, southern Nevada, New Mexico, and southwestern Utah. In the Sonoran Desert region this prickly-pear is characteristic of the upper edge of the desert, desert-oak woodland ecotone, and often occurs in oak woodland.

Figure 27 *Opuntia basilaris*. (A) Tinajas Altas, 28 Apr 2010, photo by Jim Malusa. Kofa Mts. (B) flower, near Palm Canyon, 5 Apr 2014, (C) fruit, road between Palm Canyon and Kofa Queen Canyon, 6 Apr 2014 (D) Young cladode, volunteer plant in Ajo yard, 3 Apr 2014. (E) Desiccating cladode, Horse Tank, Castle Dome Mts, 6 Apr 2014.

The fruits, comparatively smaller and drier than those of *O. engelmannii*, were probably seldom eaten if *O. engelmannii* fruits were available. Gifford (1936), however, reports that the Yavapais ate the fruits. Castetter and Underhill (1935: 16) report "an upright species of prickly pear . . . is utilized by washing the large waxy flowers to remove their sticky secretion then frying them in grease, formerly deer fat, now lard." That prickly-pear probably was *O. chlorotica*, which indeed has an upright habit.

Figure 28. *Opuntia chlorotica*. (A) N of Pinkley Peak, Puerto Blanco Mts, 31 Oct 2003. (B) Estes Canyon, 25 Apr 2013. (C) Alamo Canyon, 12 Jan 2014.

OP: Ajo Mts, 3000 ft, *Nichol 28 Mar 1939* (ORPI). Puerto Blanco and Santa Rosa Mts (Bowers 1980) Observations 1.9 mi by road N of Bates Well, N boundary of Organ Pipe, 30 Jan 1992, *Felger*, Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger*, Acuña Valley in lower foothills of western Puerto Blanco Mts, one plant seen, 30 Jan 2013, *Rutman*. †Alamo Canyon, seeds, 1150 to 32,000 ybp (7 samples) †Montezuma's Head, seeds, 13,500 to 21,840 ybp (4 samples) †Puerto Blanco Mts, on ridge, seeds, 8790 to 14,120 ybp (5 samples

CP: 7 mi E of Papago Well, *Harbison 16 Mar 1937* (SD). Observations, *Felger*. Sheep Mt, N side, mid-elevation to summit, 31 Jan 1992, Hills at E boundary of Refuge along Charlie Bell Rd, 12 & 13 Jun 1992, Agua Dulce Pass, 12 & 13 Jun 1992.

TA: †Tinajas Altas, seed, 11,040 ybp.

Opuntia engelmannii Salm-Dyck ex Engelmann
Prickly-pear, *nopal*, naw, 'i bhai

Medium-sized to large sprawling, prickly-pears, usually trunkless. Pads remaining green all year. Flowers uniformly bright yellow, becoming pale orange (apricot color) as they age, the flowers generally opening a second day. Flowering (March) April and early May. Fruit skin and pulp red-purple, the pulp sweet, juicy, and edible, fruits mostly ripen in July.

Northern Mexico and southwestern United States. Five varieties are recognized (Pinkava 2003d), with var. *engelmannii* being the most widespread.

Prickly-pears were an important food resource for the Hia Ced and other O'odham people. The young pads were harvested in late spring and summer, the spines and glochids removed, and the pads cooked as a vegetable, and the fruits eaten fresh or cooked and made into jam (e.g., Betty Melvin in Zepeda 1985; Castetter & Underhill 1935). "We would squeeze the juice from the ... fruit. ... It is better tasting than any drink. ... Early in the morning when [it] is a little cool, we would gather them. A whole box full. I would get them and squeeze the juice out ... it is so good" (Betty Melvin in Zepeda 1985: 82, 83).

1. Pads markedly elongated, more than twice as long as wide .....**Opuntia engelmannii** var. **linguiformis**

1. Pads not markedly elongated, to about 1.5 times longer than wide.

2. Branches often sprawling or spreading; spine color various, often ashy gray or sometimes reddish brown at the base and lighter colored (white coated) near the tip; larger spines often 3–5 per areole, mostly straight, largest spines 3–6.2 cm long...**Opuntia engelmannii** var. **engelmannii**

2. Branches commonly held well above the ground, or the plants sometimes spreading; spines bright yellow (not white coated), the larger spines often 1 per areole (seldom more than 3), often curved, largest spines 4.5–7.7 cm long. ..... **Opuntia engelmannii** var. **flavispina**

Opuntia engelmannii var. **engelmannii**
[*O. discata* Griffiths. *O. phaeacantha* Engelmann var. *discata* (Griffiths) L.D. Benson & Walkington]
Desert-prickly pear. Figure 29.

Robust prickly-pears, trunkless or nearly so, usually spreading or sprawling, sometimes reaching 1–1.8 m in height, the larger colonies sometimes reaching 3–4+ m across. Pads obovate to elliptic, (18) 20–33 × 16–23 cm, and about 1 cm thick, remaining green all year. Spines often 3–5 per areole, the larger ones 3–6.5 (7.7) cm long, straight or curved, yellowish to red-brown, often bleaching white with age; spine-bearing areoles often extending to the base of the pad. Flowers often 7.5–9.5 cm wide; inner tepals uniformly bright yellow, becoming yellow-orange (apricot color) as the flowers age (usually the second day); filaments and anthers pale yellow, the style white, the stigma green; flowering in spring, mostly April and May (at the same times as *O. phaeacantha*). Fruits 5.5–7.5 × 3.5–4 cm, reddish purple including the pulp, the pulp juicy and sweet, ripening in late July and August. $2n = 66$ (Baker et al. 2009).

Widely scattered in Organ Pipe and the eastern part of Cabeza Prieta including the Agua Dulce and Growler Mountains; above 1650 feet on desert flats, bajadas, pediments, hills and mountains. Above 3400 feet in the Ajo Mountains this species commonly occurs with *Juniperus arizonicus*, *Simmondsia chinensis*, and *Vauquelinia californica*. "Fruits and pads relished by rodents and other mammals including javelinas" (Simmons 1966: 102).

Texas to southwestern Utah and southern California and southward to the adjacent border states in Mexico.

OP: W side of Ajo Mts, *Nichol Mar 1939* (3 sheets, ARIZ 64930, 83680, & 135545). Alamo Canyon, *Nichol 1 May 1939* (ORPI, POM/RSA). 10 mi on road east from Headquarters, 2500 ft, 14 Nov 1955, *Benson 15615* (3 sheets each accessioned as POM/RSA 284081). S end Sierra Santa Rosa, 22 May 1989, *Baker 7761* (ORPI). Quitobaquito, old fields, 11 Aug 1990, *Felger 90-430*. Observations, *Felger*. 0.2 km W of Hwy 85 at N boundary of Monument, 23 May 1991; Hocker Well, 3 Dec 1990.

CP: Bluebird Mine, 1800 ft (Simmons 1966). Observations, *Felger*. Agua Dulce Pass, 12 & 13 Jun

1992; S of Charlie Bell Road on road to Lower Well; Childs Mt, 2400 ft, 18 Aug 1992; *Malusa* Near Temporal Pass, Growler Mts, UTM (Zone 12N), 3573000 E, 309700 N (NAD 1927), 1800 feet, 19 Feb 2000.

Opuntia engelmannii var. **flavispina** (L.D. Benson) B.D. Parfitt & Pinkava
[*O. phaeacantha* var. *flavispina* L.D. Benson]
Yellow-spine prickly-pear Figure 30.

This prickly-pear is distinguished from var. *engelmannii* by having the branches held well above the ground and the plants generally with a more erect habitat and not sprawling, with relatively fewer, often longer spines (4.5–7.7 cm long), often curved and bright yellow (not white coated), often 1 or 2 per areole (seldom more than 3 large spines per areole), the spines arching downward, and often larger fruits. Flowers similar in size and color to those of variety *engelmannii*. Records from the 1980s and 1990s document plants of this prickly-pear to 1.5 m tall, but following the severe drought of the 2000s, Sue Rutman has not seen them this large, at least not in Organ Pipe.

Figure 29. *Opuntia engelmannii* var. *engelmannii*. Mouth of Alamo Canyon, Ajo Mts. (A) 18 Nov 2003; (C) 25 Apr 2013; (D) 21 May 2006. (B) Lukeville, 5 Sep 2013. (E) Near Armenta Ranch Road E of Hwy 85, 31 Jul 2013.

This rather distinctive variety occurs in relatively small populations in the Ajo Mountains, at Quitobaquito and scattered westward along the northern edge of the Río Sonoyta in Sonora to the vicinity of Corner Well, and near prehistoric sites such as Agua Dulce Pass. Sue Rutman found one plant in 2011 about one mile north of Dos Lomitas near a prehistoric trail from Mexico to Sweetwater Pass.

The population at Quitobaquito in the 1990s was small, with about one dozen adult plants and seemed to be increasing due to discontinuation of cattle grazing. The plants were vigorous and juvenile plants were present (Felger et al. 1992). However, in the decade preceding 2014, plants at

Figure 30. *Opuntia engelmannii* var. *flavispina*. International boundary W of Quitobaquito. (A) 5 Sep 2013, (B) 13 Sep 2006, (C) 26 Aug 2013, (D) 22 Apr 2008.

Quitobaquito and westward were barely surviving due to drought. This prickly-pear occurs at former O'odham village and farming areas and may represent introduction and/or selections by the local people (Felger et al. 1992). Variety *flavispina* and var. *engelmannii* plants occur intermixed without apparent intermediates.

Variety *flavispina* is known only from southern Arizona in Maricopa, Pima, and Yavapai Counties and Sonora near the flora area (near the northern edge of the Río Sonoyta).

OP: Alamo Canyon, 2300 ft, *Nichol 27 Apr 1939* (isotype ORPI). Quitobaquito Springs, 1100 ft, shrub to 1.5 m tall, 2 m broad, fruit purple-red, 17 Aug 1988, *Baker 7625* (ASU, ORPI). Quitobaquito, old fields, 11 Aug 1990, *Felger 90-431*. Hocker Well, 3 Dec 1990, *Felger* (observation). Quitobaquito Springs, 300 m N of Mexico, in the vicinity of the spring, 1080 ft, shrub 1m tall, as broad, with leaning trunk, main spine pale yellow-brown, to 7 cm long, others twisting and curving, several plants in area, mostly smaller, $n = 33$, 19 Mar 1992, *Baker 8788* (ASU, cited in Haseltonia 6: 35, 1999).

CP: N slope of Agua Dulce Mts, along road 0.3 mi below Agua Dulce Pass, 1550 ft, granitic rock, rare, 1.5 m tall, the branches held well above the ground, dry [old] fruits red-purple, 14 Sep 1992, *Felger 92-737* (ASU, DES).

****Opuntia engelmannii** var. **linguiformis** (Griffiths) B.D. Parfitt & Pinkava
[*O. linguiformis* Griffiths]
Cow-tongue prickly-pear. Figure 31

Large, sprawling plants, propagating vegetatively, and distinguished by markedly elongated stem segments of indeterminate growth. Flowers large and yellow, the plants apparently sterile.

Cultivated at Lukeville and Sonoyta and sometimes becoming weedy. Large pieces of this unattractive cactus dumped in the desert as trash are the sources of the plants east and west of Lukeville, less than 200 m north of the international border. The plants seem to persist but apparently are not spreading.

Figure 31. *Opuntia engelmannii* var. *linguiformis*. Lukeville. (A) 30 Oct 2003, (B) 21 May 2006.

This prickly-pear is widely cultivated and is sometimes feral in southern Arizona (perhaps resulting from trash-dumped plants). Also in southern New Mexico, southern Texas, and northern Mexico. No native populations are known for certain (Anderson 2001; Parfitt & Pinkava 1988; Pinkava 2003d). A cultivated individual from east of Tucson was a pentaploid, $2n = 55$ (Baker et al. 2009); all other counts in the literature for this taxon have been hexaploid.

OP. Observations, 3 Nov 2003, *Rutman*. Within 1 mi E of Lukeville and less than ¼ mi N of the international boundary, between Lukeville and Gachado Line Camp, few dozen plants, growing from dumped plants; About ½ mi N of Lukeville on Hwy 85, 100 ft W of highway in a grove of *Prosopis* & *Atriplex*, Less than a few hundred feet N of the international boundary, dissected hills between Lukeville and Dowling Ranch, several plants.

†Opuntia engelmannii and/or **O. phaeacantha**

We are not able to distinguish these two prickly-pears with fossil seeds.

OP. †Alamo Canyon, seeds, 1150 to 32,000 ybp (6 samples). Puerto Blanco Mts, on ridge, seeds, 980 to 7970 ybp (5 samples; *O. engelmannii* var. *engelmannii* presently occurs in washes below the midden site, but not on the rocks at the midden site)

Opuntia engelmannii and *O. phaeacantha* may hybridize and the resulting variation can be perplexing. For example, *O. phaeacantha* plants known to have red-centered flowers can also have fruits with red-colored rind, the pulp being whitish or even reddish. Sometimes the hexaploid *O. engelmannii/phaeacantha* complex can be seen as a super species or species complex, with no hard and fast rules, only trends, and the trends can be localized. Some cactus enthusiasts and botanists have recognized dozens of species within the complex, many of which are probably apomictic clones or microspecies. In the flora area as well as elsewhere, *O. engelmannii* and *O. phaeacantha* often occur together. The morphology at both ends of the gamut is so different that people have a difficult time not wanting to keep them as separate species. Perhaps DNA studies will eventually help clarify the problem. For example, David Griffiths (1867–1935) named more than a dozen species at both ends of the gamut as well as morphological intermediates in many localities based on minor differences. Some people have picked up these names and claim they can identify them and perhaps they can but the question is: Are they worthy of taxonomic recognition and, if so, is there any way to make a key so that you or I or anybody else can identify them? The problem may be likened to that of the dog, where there are a myriad of forms but all belonging to the same species.

Opuntia phaeacantha Engelmann

Brown-spine prickly-pear; *nopal*. Figure 32.

Low, spreading prickly-pears, sometimes to 0.5 m tall, generally much wider than tall, often forming trailing stems of several or more pads. Pads becoming moderately reddish purple in winter and spring. Areoles often bearing long, stout, and sometimes darkish and spreading spines. Young central spines usually reddish brown, becoming ashy gray with age. Central spines usually lacking or much reduced on the lower (proximal) part of the pads. Flowers, especially when first opening, yellow with a reddish-orange center; flowering in April and May. Fruits ripening in July.

Eastern part of Organ Pipe; upper and middle bajadas and less common on lower slopes of the Ajo and Diablo Mountains. Often growing with *O. engelmannii*. Also common northward from Organ Pipe in some areas of the Sauceda, Sikort Chuapo, and Sand Tank Mountains.

A highly polymorphic species; California to Kansas and Texas and northern Mexico.

The fruits of this species are generally smaller, less juicy, and much less desirable for eating than *O. engelmannii* fruits (Felger 2007; Pinkava 2003c). Castetter and Underhill (1935: 22) report

that the O'Odham (Papago) "distinguish two kinds of edible prickly pears (*Opuntia* sp.), one of which produces chills and nausea in susceptible people." This statement likely refers to *O. phaeacantha*, while the other kind is probably *O. engelmannii*.

Although the differences between *O. engelmannii* and *O. phaeacantha* are subtle and perplexing, they usually can be distinguished in the flora area using a suite of key features. *Opuntia phaeacantha* tends to form shorter and more sprawling plants, the stems often trailing, and there are differences in the pattern of the glochids in the areoles (Pinkava 2003c, d). Sue Rutman finds two main field characters when the plants are not blooming: First, the central spines are absent or reduced on the lower third of the cladode in *O. phaeacantha*, while central spines extend to the base of the pad in *O. engelmannii*. Second, the shape of the *O. phaeacantha* pad is more elongated than the rounder (circular) shape of *O. engelmannii*. The Organ Pipe and Sauceda Mountain populations of *O. phaeacantha* generally have long and more obviously spreading and rather dark spines, and in winter

Figure 32. *Opuntia phaeacantha*. Mouth of Alamo Canyon, Ajo Mts: (A & B) 25 Apr 2013; (C) 21 May 2006; (D) 27 Jan 2009, (F) 27 Jan 2009. (E) Near Ryan Wash, Sauceda Mts, 4 Aug 2013.

and the spring dry season the pads tend to become purplish or brownish at least in part. The bicolored flowers (yellow with a reddish center) provide a clear-cut diagnostic distinction, and are evident as soon as a flower opens. The flowers (tepals) of both species become yellow-orange or peach-colored as they age, even during the afternoon of first day if the weather is hot, and probably always on their second day, which can obliterate the ability to distinguish these two prickly-pears. Flowers of *O. phaeacantha* can be smaller than those of *O. engelmannii*. The fruits of *O. phaeacantha* tend to be narrow and cylindroid, typically the "skin" is dull pinkish (pinkish orange in the extreme form) or brick red, and the pulp is typically lighter in color, not purple-staining, and not especially juicy (but "over-ripe" fruits can become juicier and redder), and the pulp not sweet and not very good to eat. In contrast the fruits of *O. engelmannii* are plumper, generally larger, and more egg-shaped, and the "skin" and pulp brilliant, dark purple, beet red, or burgundy, and the pulp decidedly sweet and juicy.

OP: Boulder Canyon, 3500 ft, 24 May 1962, *Steenbergh S-2482-5* (POM/RSA) 0.5 mi N of Alamo Canyon campground on Alamo Canyon road, with *O. engelmannii*, *Rutman 26 Apr 2002*. Gunsight Hills, 14 Mar 2003, *Rutman 2003-535* (ARIZ, ORPI). Flowers from part of same plant as *Rutman 26 Apr 2002*, grown in Tucson, *Felger 14 May 2005*

****Opuntia santa-rita** (Griffiths & Hare) Rose
Purple prickly-pear

Upright-growing prickly-pear, often reaching about 1 m tall. The pads become purplish during cool and dry seasons. An attractive plant, often cultivated.

A specimen labeled Quitobaquito is likely to be from a cultivated plant, and seems to be the source of Benson's (1982) mapping of this species in Organ Pipe (Felger et al. 1992).

OP: Quitobaquito, *Nichol 27 Apr 1939* (ORPI).

Peniocereus – Night-blooming cereus

Slender-stemmed cacti with tuberous roots. Stems appearing cryptic, mimicking shrub and tree branches. Areoles with relatively small spines, the central and radial spines similar; areole glands none. Oldest stems at base of plants becoming woody and without fleshy tissue. Flowers (those in the flora area) relatively large, white, nocturnal, and fragrant; adapted for pollination by hawk moths (Sphingidae). Fruits red and juicy. This genus as a natural (monophyletic) group includes 7 species in Mexico (Arias et al. 2005), 4 of which occur in the Sonoran Desert, and 2 of them range into southwestern USA.

Only a relatively few species in the entire cactus family have truly tuberous roots, which seems rather surprising, and they all have rather small stems (Mauseth 2014; Stone-Palmquist & Mauseth 2002). Seven Sonoran Desert cacti have conspicuous tuberous roots. Six occur in Sonora: *Echinocereus leucanthus* N.P. Taylor, *Grusonia marenae* (W.E. Parsons) E.F. Anderson, *G. reflexispina* (Wiggins & Rollins) E.F. Anderson, *Peniocereus greggii*, *P. mariamus* (Gentry) Sánchez-Mejorada, and *P. striatus*. Two occur in the Baja California Peninsula: *Peniocereus johnstonii* Britton & Rose and *P. striatus*. The four *Peniocereus* grow on fine textured lowland soils as well rocky habitats and sometimes even in bedrock. The *Echinocereus* and two *Grusonia* only occur on lowland, sandy or fine-textured soils.

1. Stems reaching 20 mm diameter, with 4 or 5 (rarely 6) ribs. ..... **Peniocereus greggii**
1. Stems 4.5–8 mm diameter, with 6–9 flat-topped ribs separated by narrow furrows or grooves ..... **Peniocereus striatus**

Peniocereus greggii (Engelmann) Britton & Rose var. **transmontanus** (Engelmann) Backeberg
[*Cereus greggii* Engelmann var. *transmontanus* Engelmann]
Desert night-blooming cereus, *reina de la noche, sarramatraca*, ho'ok wa', ho'isa (Betty Melvin)
Figure 33

Plants with a single large tuberous root. Stems cryptic and grayish, and seem to mimic dead branches of shrubs or trees, stems mostly few-branched, to 1.5 m tall, and about 2 cm diameter. Seedlings and youngest plants with 4 ribs, older and adult plants with 4 or 5 (rarely 6) ribs or angles, the stem surfaces purplish brown and minutely pubescent with short, whitish hairs. Flowers large (15–22 cm long) and white with a long tube, spectacularly fragrant, opening shortly after sunset and visited by pollinating hawk moths (Sphingidae), and quickly wilting after sunrise. Fruits ovoid, 10 × 4 cm, bright red throughout, the pulp juicy and sweet. Flowering occurs synchronously in a population on one to few nights in July, the fruits generally ripening August and September, and rarely persist until spring (e.g., March).

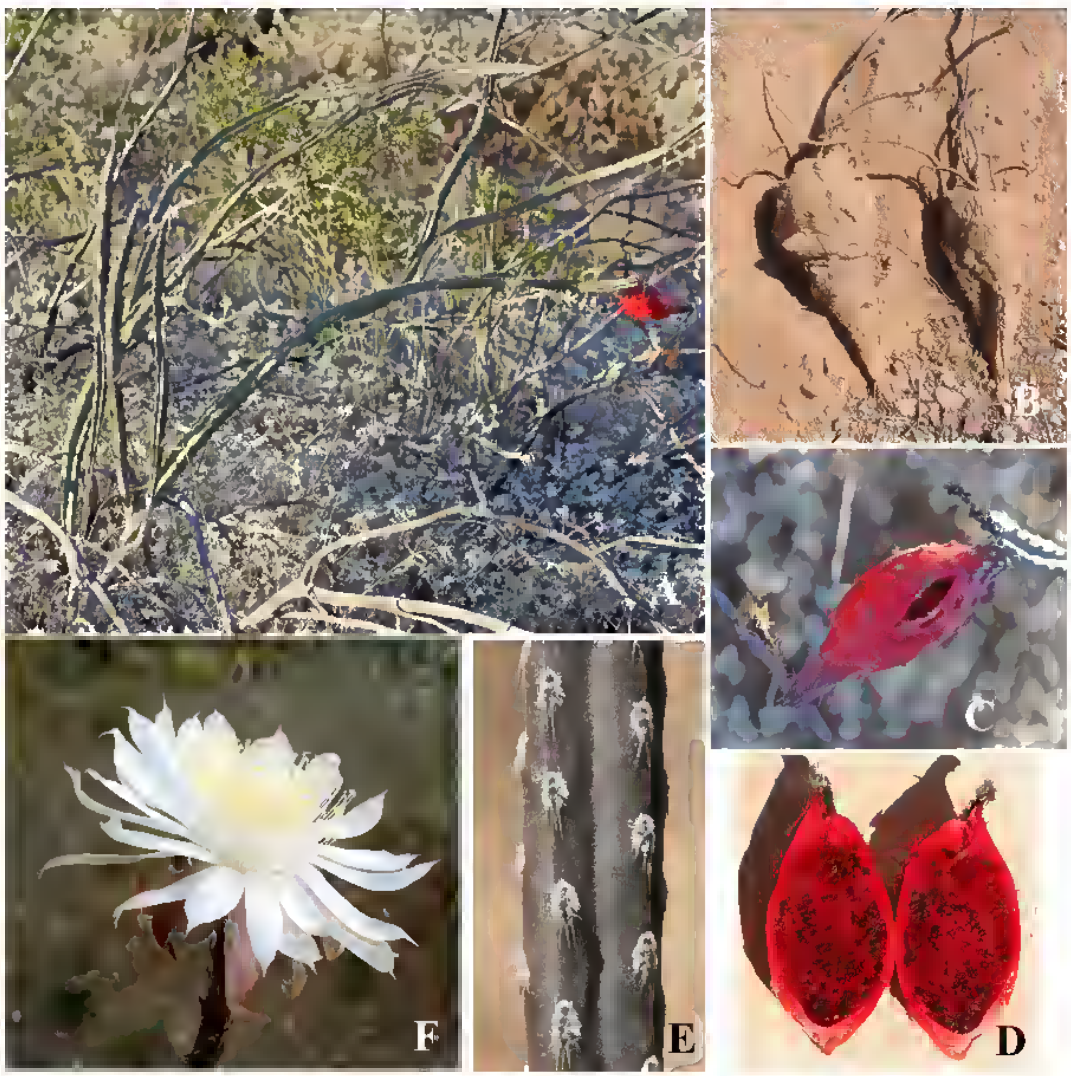

Figure 33. *Peniocereus greggii* var. *transmontanus*. (A & C) Kuakatch Wash west of Hwy 85, 6 Oct 2012. (B) Tuberous roots of plants rescued from construction site along Hwy 85, 9 Aug 2003. (D) Armenta Ranch Road, W of Hwy 85, 1 Mar 2008. (E) Dos Lomitas, 30 Sep 2006. (F) Organ Pipe visitor center, 14 Jun 2004.

Small to moderate-sized populations occur across Organ Pipe and Cabeza Prieta, mostly in the lowlands, separated by large unoccupied areas, and also in the Tinajas Altas Mountains. Creosotebush flats, bajadas, wash margins, canyons, and rocky slopes. Often growing in the shelter of desert shrubs, but sometimes also found in open areas (perhaps nurse plants were once present). The plants are seldom encountered due to the cryptic nature of the stems and throughout its range it characteristically grows at low densities. The stems are susceptible to freezing, but regrow rapidly from the large tuberous root. The plants are palatable to wildlife and packrats are known to chew the stems like a Popsicle. Illegal collecting has occurred in Organ Pipe along the US/Mexico border near populated areas.

Variety *transmontanus* is largely a plant of the Sonoran Desert in southern Arizona and northwestern Sonora. Variety *greggii* is a Chihuahuan Desert taxon, in southeastern Arizona, southern New Mexico, west Texas, Chihuahua, northeastern Durango, Coahuila, and Zacatecas.

The root has been used medicinally for diabetes and respiratory ailments, and the fruits eaten fresh (Felger et al. 1992). In his field notebook (Mearns 1892–93) recorded this: "The root is a large tuber, like a yam. In much repute as a remedy for syphilis throughout northwest portion of Mexico." Betty Melvin (in Zepeda 1985: 78–79) reported, "Well you get the root, and then you peel it. . . . and you wash your hair with it. . . . you peel them and you cut them up and they taste like. . . cucumbers. You eat it with meat. Ho'isa, that's the name." Castetter and Underhill (1935: 18) reported that the tuberous root was "chewed raw for thirst or . . . baked whole in ashes, peeled and eaten." Castetter and Underhill also claimed that the "stalks" were eaten, but that seems improbable.

OP: Bates Well, *Nichol 27 Apr 1939* (ORPI). 9 mi W of Visitor Center, N end of Puerto Blanco Drive, desert flats, 25 Nov 1972, *Pinkava 10034* (DES). Vicinity of Aguajita Spring, 3 Dec 1990, *Felger 90-574*. W of Hwy 85 on Armenta Rd, *Anderson 15 Jul 2002* (ORPI). Observations: Dos Lomitas, 30 Apr 2002, *Rutman*; 5 mi E of Quitobaquito in *Atriplex polycarpa* flats, Jan 1990, *Robert A. Johnson*.

CP: Near Jose Juan Represo, 12 Jun 1992, *Felger* (observation). Near Tule Tank, 5 Mar 1995, *Rebman 2890* (ASU). Western Tule Mts, rooted in bedrock, 25 Nov 2003, *Rutman* (photo).

TA: Tinajas Altas. 21 Feb 1894, *Mearns 2811* (DS, US), 6 Mar 1937, *Harbison 16828* (SD). E end Tinajas Altas Pass, 12 Feb 1977, *Reeves 5396* (ASU).

Peniocereus striatus (Brandegee) Buxbaum

[*Cereus striatus* Brandegee. *Wilcoxia striata* (Brandegee) Britton & Rose. *Neoevansia striata* (Brandegee) Sánchez-Mejorada. *Cereus diguetii* F.A.C. Weber. *Wilcoxia diguetii* (F.A.C. Weber) Diguet & Guillaumin]

Dahlia-root cereus; *sacamatraca, sarramatraca*; 'i:kuli. Figure 34.

Plants often 0.6–1.5 m tall and much branched above. Stems 4.5–8 mm diameter (1–2 years old), at first greenish with minute hairs, soon becoming brownish or grayish and glabrous, with 6–9 flat ribs separated by deep furrows or grooves, the stomata restricted to the grooves. Each plant may produce a dozen or more potato-like tuberous roots strung on clusters of slender connecting roots. (Plants in southwestern Sonora sometimes have up to 70 or more tuberous roots.) Areoles circular, ca. 1 mm diameter; spines 5–15 per areole, 1–5 mm long innocuous and bristle-like, mostly soon deciduous, (spines on floral tube and fruits much longer), white or brown-tipped, and closely appressed to the stem. Flowers nocturnal, about 9–11 cm long, 8+ cm wide, with a slender tube, the inner tepals white or moderately rose-tinted; pollinated by hawk moths (Sphingidae). Fruits about 5 cm long, ovoid, the ripe pulp red, juicy, sweet and edible, the rind red when ripe, with short bristly spines on small, sparsely distributed and deciduous areoles. Seeds 2–2.5 mm long, dark red-brown to blackish. Flowering in summer, the fruits ripening late summer and fall. Most of the plants show recovery from freeze-damage and herbivory.

Figure 34. *Peniocereus striatus* and *Euphorbia cryptospinosa*. *P. striatus*: (A) Bush-like form, Dos Lomitas, 15 Nov 2002, (B) 24 Oct 2007, photo by Jergen Mentzel (SEINet); (C) ripe and near ripe fruit, Dos Lomitas, 15 Nov 2011; (D) tuberous roots, Dos Lomitas, NPS-ORPI photo, 1940s, (E) Dos Lomitas, 15 Nov 2002, photo by Greta Anderson, (F) cross-section of stem, cultivated plant, originally from vicinity of Sonoyta, Sonora, 14 Aug 2013, photo by Elroy Limmer. *E. cryptospinosa*: (G & H) Cross-section of stem and portion of stem near apex with flower clusters (cyathia), cultivated plant, originally from Kenya, 14 Aug 2013, photos by Elroy Limmer.

Highly localized in the southeastern part of Organ Pipe near the international boundary where it is at its northern geographic limit, and farther east along the southern margins of the Tohono O'odham lands. There are no other populations in the United States (Felger & Zimmerman 2000; Rutman & Anderson 2007). The main population is in northwestern Mexico where it is widespread and sometimes locally common in western Sonora, northwestern Sinaloa, Baja California Sur, southern Baja California, and a number of Gulf of California islands (Felger & Wilder 2012; Suzán et al. 1994). The tuberous roots have been used medicinally (Felger & Moser 1985; Hodgson 2001).

Greta Anderson conducted an extensive study of this cactus in Organ Pipe from January to July 2002 (Anderson et al. 2010). Her study, covering 177 ha, included the known distribution within the Monument, which has been censused occasionally since 1939. Anderson found two growth forms among the Organ Pipe plants: vine-like and bush-like. Vine-like plants often scramble through spiny shrubs such as *Lycium* and tree branches for support, and can reach several meters across. Bush-like plants are sometime in open areas (not among a nurse plant, or perhaps the nurse plants has since perished) and the stems of such plants tend to show more than usual freeze-damage. The study resulted in the discovery of 88 new plants, in addition to the relocation of 57 plants found in previous surveys (Johnson et al. 1990). Mean height and width of the plants was 58.6 cm and 54.4 cm, respectively, the majority being 40–80 cm tall, and maximum height and width 158 and 304 cm, respectively. Despite potential increases in population size and spatial distribution, mean plant height and number of basal stems had not significantly changed in recent years. *Peniocereus striatus* occurrence increased with decreasing slope, spanned every slope aspect, and was highest on rocky temperature at the site dropped to -13.7ºC, top-killed 19% of the population, with the greatest damage in drainage bottoms. However, long-term (1944–2002) climate records show that there has been an overall increase in the number of frost free days in the region, which, coupled with land use change, has implications for the future health of this population." By early summer 2002, more than half of top-killed plants had re-sprouted from the base or had new branches growing from the desiccated stems.

Greta's study came to an abrupt end on August 9, 2002 when her vehicle at the *P. striatus* site was vandalized by fugitives from Mexico on the day National Park Service Ranger Kris Eggle was murdered by one of the same two armed fugitives who had fled across the border into Organ Pipe. From Tim Tibbitts (13 Mar 2013): "My memory is Greta's incident was a couple hours before Kris was killed. I was at work, driving up out of Growler Pass, and heard it over the radio. I talked to Greta on the radio, drove to HQ, looked at her truck which had the window smashed out, spoke with Bo Stone, one of our law enforcement staff at that time, about getting the incident report taken care of. Around 1:00 pm, I headed north toward Ajo on the highway, headed home. Unbeknown to me (because I'd turned my radio off, in Off-Duty Friday mode), at about that time the shooting incident was playing out near Gachado."

The 2010 publication is dedicated to National Park Service Ranger Kris Eggle (1973–2002).

OP: 8 mi NE of Sonoyta, Sonora, 1400 ft, *Nichol 20 Apr 1939* E of Lukeville, 1450 ft, *Nichol 4 May 1939* (ORPI) Dos Lomitas, 1500 ft, W-facing rocky hillside, with *Cereus thurberi, C. giganteus, Larrea tridentata, Ambrosia deltoidea*, growing in and among *A. deltoidea*, 63.5 cm tall, 16 Aug 1988, *Baker 7621* (ASU)

Sonora: 6 km E Sonoyta, cerca de la frontera con Organ Pipe Cactus National Monument, laderas rioliticas, 31°52'N, 112°45'W, 438 m, *Larrea tridentata, Encelia farinosa, Olneya tesota, Cercidium microphyllum*, 21 Oct 1993, *Suzán 333* (ASU)

CONVERGENT EVOLUTION OF *PENIOCEREUS STRIATUS* AND AN AFRICAN *EUPHORBIA*

The unusual stem morphology of *Peniocereus striatus* shows remarkable convergent evolution with *Euphorbia cryptospinosa* Bally (Euphorbiaceae), a spurge known from arid regions in Ethiopia, Somalia, and Kenya (Felger & Henrickson 1971; figures 34–37). These similar appearing succulents share water-conserving adaptations. The cactus and the euphorbia both have slender pencil-like stems with stomata restricted to furrows separated by bark-covered ribs. As the stems shrink in drought, the ribs come together to close off the furrows resulting in a cylinder-like surface, which effectively reduces water loss and surface-to-volume ratios (figures 35 & 37). Theoretical surface-to-volume relationships in succulent plants, especially cacti, are expertly described and interpreted by Mauseth (2000) and Porembski et al. (1991).

The cactus has stems 5–9 mm diameter and 6–9 furrows. The spurge has stems 7–12 mm diameter and 4–9 furrows. Both have brownish gray stems that look like woody stems or dead twigs of the surrounding shrubs, which presumably provide protection from herbivores through camouflage. Both have tuberous roots that provide water and food-storing capacity. The cactus has areoles that bear weak spines and relatively large, dioecious, nocturnal flowers (figure 36 a–d). The spurge bears only two spines (modified stipules), about 1.5 mm long at each node, is monoecious, and bears clusters of scarlet-colored cyathia near the stem-apex (Figures 34 G & H; 36 e–i).

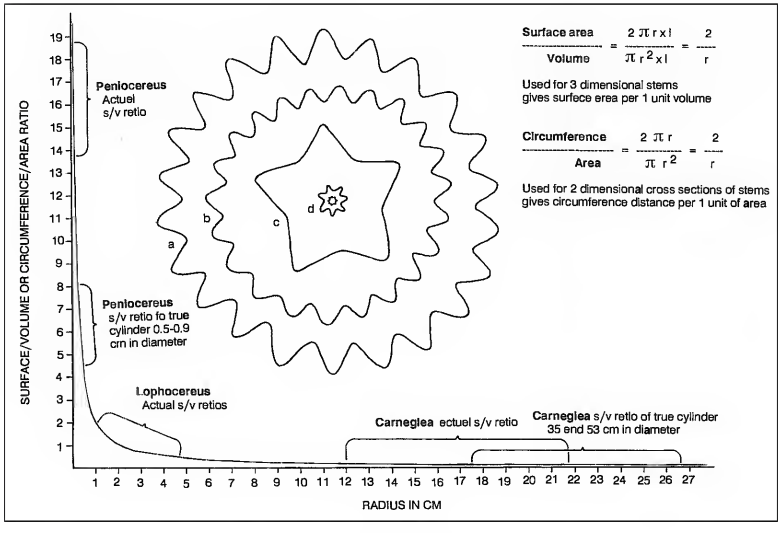

Figure 35. Relationship of surface/volume ratios and stem sizes. Formulas for determining three-dimensional surface/volume ratios and two-dimensional circumference/area ratios are shown at upper right. The curve on the left and bottom margin shows the relation between s/v ratio (ordinate) and stem size (as radius in cm, abscissa). (a–d) Outlines of various cacti from which s/v ratios have been determined: (a & b) *Carnegiea gigantea*: (a) larger stem; (b) smaller stem. (c & d) *Lophocereus schottii* showing extreme variation in stem sections from northern (c) to southern (d) populations (from Felger and Lowe 1967). An outline of a *Peniocereus striatus* stem is shown within d. The range of s/v ratios for the three cacti is shown along the regression curve. (From Felger & Henrickson 1997).

Numerous structural similarities exist at the microscopic level. In both, the ribs are covered with thickened, suberized, translucent periderm. The outermost cortex contains layers of collenchyma that are much thicker under the ribs than under the furrows. Collenchyma tissue in both species contains reddish pigment that darkens the outer stems, aiding in camouflage. The inner mass of cortex consists of parenchymatous water-storage tissue, while starch is stored in the pith.

In both species phellem (true bark) of successive seasons is eventually lost, falling away by means of an abscission layer comprised of thin-walled, non-collapsed cells that are the last-formed cells of the previous season's growth. Also in both species the consistent radial orientation of the phellem cells of successive seasons indicates that either the same phellogen is active over several seasons or new phellogens are derived from the phelloderm. The underlying lamellar collenchyma tissue present in both taxa consists of one or two layers (to 50 μ thick) of cells of dimensions similar to those of their respective phellem cells. Interior to the collenchyma tissue, parenchymatous cortex tissue contains chloroplasts that are more numerous under the ribs than under the adjacent furrows. Structure of the furrow region is distinct from that of the ribs, as the epidermis is persistent and is not replaced by more rigid periderm.

Yet the two species differ in many anatomical details. The rib periderm of *Peniocereus striatus* ranges from 35–50 μ in thickness and consists of tabloid cells 35–140 μ long and 30–40 μ wide, with moderately thickened walls. Rib periderm in *E. cryptospinosa* is slightly thicker (50–75 μ) and consists of longer, fiber-like cells to 450 μ in length, 25–50 μ maximum width, with uniformly thin walls.

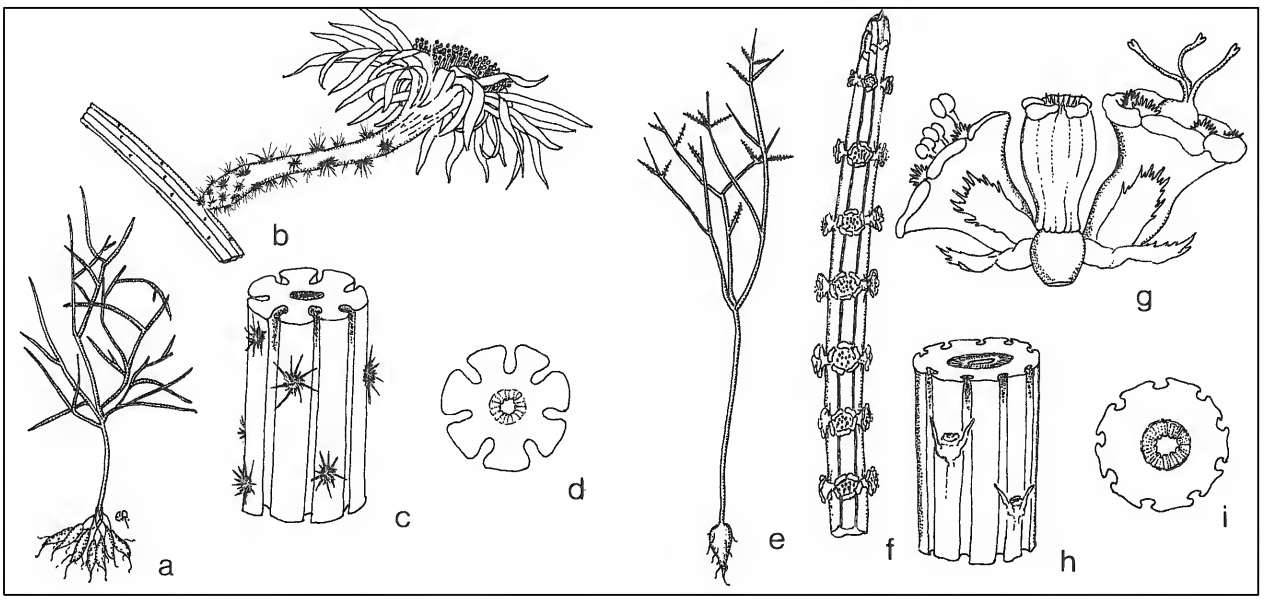

Figure 36. *Peniocereus striatus* and *Euphorbia cryptospinosa*. *P. striatus*: (a) growth habit; (b) stem with flower; (c & d) stem and cross section showing central xylem and stomata-containing furrows. *E. cryptospinosa* (redrawn from Bally 1963): (e) growth habit showing a single turnip-like storage root and branched stems; (f) distal portion of stem showing cyathia; (g) triad of cyathia, cyathium at left shows staminate florets (anthers) and cyathium at right shows a pistillate floret; (h) portion of stem showing paired stipular spines at nodes and distinctive furrows; (i) cross section of stem, showing central xylem and stomata-containing furrows. (From Felger & Henrickson 1997).

Minor structural differences are also apparent in the furrows. In *Peniocereus striatus* the outer epidermal cell walls are much thicker (14 μ) than the inner (3 μ) walls, with a thin cuticle measuring only 2 μ in thickness. Epidermal cell walls of *E. cryptospinosa* are also thickened but are

considerably thinner (2–6 μ), while the cuticle is thicker (4 μ). The furrows of *P. striatus* are glabrous, while those of *E. cryptospinosa* are beset with short, blunt, biseriate trichomes to 80 μ long.

Stomata in both species are restricted to the furrow areas, with paracytic subsidiary cells. However, the cactus averages 48 stomata per mm^2, while there are 88 stomata per mm^2 in the spurge. Stomata along the furrow margins in desiccated stems of *Peniocereus striatus* are completely sealed over by an undetermined substance (perhaps a polysaccharide) that was removed by washing with water. This substance should be significant in reducing water loss during drought.

It's obvious that the internal volume of all succulents changes during wet and dry times or seasons. Expansion and contraction of stem volume typically alters the shape of the plant, e.g., ribs narrow, tubercles flatten or narrow, or, in most prickly-pears the entire stem flattens. The surface area remains approximately constant while the internal volume decreases, resulting in gradually increasing s/v ratios. But the stems of *Peniocereus striatus* and *E. cryptospinosa* provide a notable exception. During drought, volume (measured as stem cross-sectional area) decreases as expected. However, unlike other succulents, the effective surface area (circumference of the exposed area) also decreases as a result of the reduction of effective exposed surface area as the ribs close off the furrows. If the furrows are not closed off, the surface area in desiccated stems remains nearly unchanged and the s/v ratios would be 34–44 percent greater than those encountered. Moreover, because the exposed surfaces in the desiccated state primarily consist of impermeable periderm, the actual water loss is even less than might be expected from the s/v ratio alone.

It's remarkable that these two species have similar gross morphology, while each is distinct at the microscopic level. In desiccated stems of *Peniocereus striatus*, stomata at the margins of the furrows are sealed over by an unknown, water-soluble material. A similar phenomenon is seen in *Calabanus hookeri* (Nolinoideae, Asparagaceae), where similar water-soluble material fills stomata-containing furrows in the leaves of water-deprived plants. In contrast, furrows of *E. cryptospinosa* contain series of short, blunt trichomes or papillae that are similar in size and appearance to those found in such diverse semi-succulents as Joshua tree (*Yucca brevifolia*) and mistletoes (*Phoradendron brachystachyum* [*P. diguetianum*] and *P. flavescens*). These papillae are expected to provide reduced air movement within the furrows, thereby reducing transpiration by preventing mixing of dry air with the more humid air within the furrows.

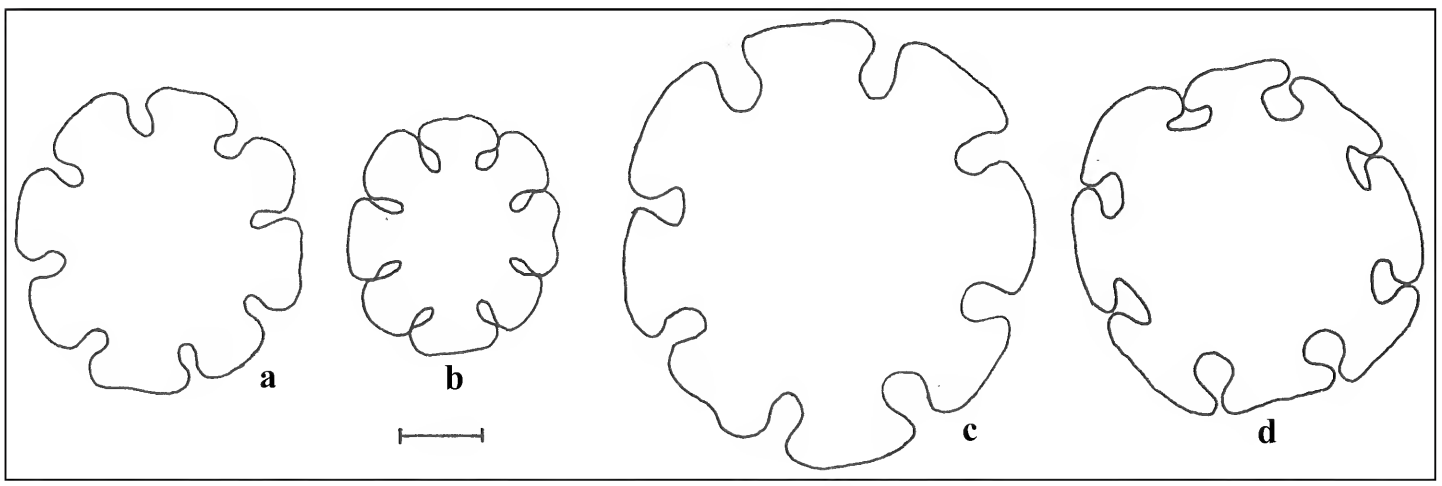

Figure 37. Outlines of hydrated vs. desiccated stems of *Peniocereus striatus* and *Euphorbia cryptospinosa*. *P. striatus*: (a) hydrated stem showing open furrows; (b) desiccated stem showing closed furrows. *E. cryptospinosa*: (c) hydrated stem showing open furrows; (d) desiccated stem showing closed furrows; bar = 2 mm. (From Felger & Henrickson 1997).

The stem structure displayed by *Peniocereus striatus* and *E. cryptospinosa* also occurs in other plants. Other related cacti also have narrow, furrowed stems, namely *Peniocereus lazaro-cardenasii* (J.L Contreras et al.) D.R. Hunt, *P. viperinus* (Weber) Buxbaum, and *P. zapilotensis* (Meyran) Buxbaum. Similar furrows and ridges are found in species of, trailing to climbing cacti ranging from Texas to northern South America. Stems of *S. murrillii* Britton & Rose have 7–8 periderm-covered ribs and the stomata are restricted to the furrows as in *P. striatus*. A number of East African spurges have similar stem morphology to that of *E. cryptospinosa* and *P. striatus*, e.g., *Euphorbia asthenacantha* S. Carter (Tanzania), *E. erlangeri* Pax (northeastern Kenya), *E. mignurtinorum* Chiovenda (eastern Ethiopia), *E. ataruensis* S. Carter (southeastern Kenya) and probably more (Bally 1963; Peter Bally pers. comm. to Felger, 1996; Robert Webb, pers. comm. to Felger, 2014; also see Carter 2001). *Euphorbia cryptospinosa* becomes a large shrub in the wild and the others are much smaller and likely to more closely resemble *P. striatus*. Also see comparative information for saguaro (*Carnegiea*) and senita (*Lophocereus*) (figure 35).

Sclerocactus – Pineapple Cactus

Small, usually globose or cylindrical plants. About two dozen species in southwestern United States and Mexico. Comparative DNA sequencing by Mark Porter at Ranch Santa Botanical Garden indicates that species of *Echinomastus* should be placed within *Sclerocactus* (Porter et al. 2000; also Porter & Anderson 2011).

Sclerocactus johnsonii (Parry ex Engelmann) N.P. Taylor

[*Echinocactus johnsonii* Parry ex Engelmann. *Echinomastus johnsonii* (Engelmann) E.M. Baxter. *E. acunensis* W.T. Marshall, Saguaroland Bull. 7: 33, 1953. *E. erectocentrus* (J.M. Coulter) Britton & Rose var. *acunensis* (W.T. Marshall) Bravo. *Neolloydia erectocentra* (J.M. Coulter) L.D. Benson var. *acunensis* (W.T. Marshall) L.D. Benson. *See* Baker (2012b) for detailed listing of synonyms and publications.]

Johnson's dwarf barrel cactus, Johnson's bee-hive cactus. Figure 38.

Dwarf barrel cactus, usually with a solitary, nearly ovoid to ovoid-cylindroid stem, 6.5–13 (27) × 6.5–8.5 cm, with 21 prominently undulate ribs. Spines obscuring the stem surface; central spines (1) 2–3 (4) per areole, ascending and slightly curved, 2.5–4.4 cm long; radial spines 13–15 per areole, straight, spreading close to the stem. Areoles bearing 1 (2) pale yellow-brown glands, these to 1.5 mm diameter, and attended by ants. Flowers showy, 3.5–6 × 4–9 cm. Inner tepals 13–21 in number, (2) 3–4 × 0.75–1.5 cm, bright rose-pink with pale margins (varying somewhat in hue from plant to plant), basally blotched with maroon or chestnut extending 30–45% of the length of the tepal. Filaments yellow-green (chartreuse), contrasting with the rest of the flower; anthers pale yellow. Stigma lobes 10–13, pink to dull red, covered with unicellular papillae of bright green, brownish green, or pale golden green. Fruits 1.5–2 cm long, ellipsoid-cylindroid, greenish and slightly glaucous, moderately fleshy, dehiscent through vertical splits (often indehiscent on drought-stressed plants), and quickly drying; receptacle bracts scale-like, the margins erose. Seeds dark red-brown (nearly black), 2–2.3 × 1.6–1.9 mm, the surfaces regularly and minutely papillate; seeds with or without a very low dorsal crest. Flowering mid-March and early April; fruits ripening in April. The plants are self-incompatible and effective pollinators are several species of native bees.

This cactus is rare in Organ Pipe, where it is usually found on bedrock or thin soils, or occasionally on well-drained alluvium or colluvium, (Johnson 1992; Johnson et al. 1993). Most of the plants are found on open, exposed situations. In nearby Sonora the young plants are often found beneath small shrubs as well as at the base of larger *Sclerocactus* plants, which serve as nurse plants, and the plants are generally more robust in partial shade of nurse plants than in open sites (Felger & Zimmerman 2000). Sue Rutman found that seeds can be viable for several years. The numbers of this cactus have precipitously declined in Organ Pipe, most likely due to drought and stem damage

Figure 38. *Sclerocactus johnsonii*. Ajo, Pima Co. (A) Young plants established from seeds, at base of mother plant, east of Ajo mine pit, 19 Mar 2006, (B) 27 Mar 2010, (C) 11 Mar 2014, (D) spherical form of juvenile plant, (E) dry fruit, 23 May 2010, (F) 27 Mar 2010.

by boring insect larvae. Other sources of mortality are predation of seeds and fruits (by insects and birds), and loss by herbivory (perhaps by packrats, etc.), curved-bill thrashers uprooting plants, and poaching by cactus collectors (Organ Pipe Cactus National Monument 2011).

Arizona (widespread but spotty), northwestern Sonora, southern California (Mohave Desert), southern Nevada, and southwestern Utah.

Recent morphological evidence does not support the recognition of *Echinomastus erectocentrus* var. *acunensis* as a taxon unique from what we recognize here as *Sclerocactus johnsonii* (Baker 2007, 2012b). Marc Baker carried out an initial morphological analysis of *Echinomastus* in 2006 throughout most of its range in Arizona, California, and Nevada, sampling 476 individuals among 15 populations (Baker 2007). At the time of his study, populations of *E. acunensis* (basionym for *Neolloydia erectocentra* var. *acunensis*) were defined by Benson (1982) as occurring in Maricopa County south of Gila Bend; Pima County, Ajo and Organ Pipe areas; Pinal County, just east of Florence; and in northwestern Sonora. In Baker's study, discriminant function and cluster analyses placed populations of *E. acunensis* closer to those of *E. johnsonii* than to those of *E. erectocentrus*. For example, within the two southernmost populations of *E. johnsonii*, more than half of the individuals were misclassified as *E. acunensis* and there was only one individual of *E. acunensis* misclassified as *E. erectocentrus*. Since his earlier studies, Baker sampled two more populations of *E. johnsonii* (including the type localities for *E. artzonicus*, Butler Valley, Arizona, and *E. johnsonii*, near St. George, Utah) and results further supported the presence of a geographical/morphological cline from the northern Mojave Desert to the northern Sonoran Desert. Average character values, by population, for most characters decrease in value from the northwest to the southeast within the overall distribution of the populations studied. Results from this augmented analysis further support the inclusion of historical *E. acunensis* populations within *E. johnsonii* and suggest that there are no recognizable subspecific taxa within *E. johnsonii*. Although there was a fairly clear geographic and morphologic break between populations of *E. acunensis* and those of *E. erectocentrus*, there was no clear break between populations of *E. acunensis* and those of *E. johnsonii* (Baker 2012b). Based on Baker's findings, we believe that the status and final rule to list *Echinomastus erectocentrus* var. *acunensis* (U.S. Fish & Wildlife Service 2013) should be reviewed.

OP. Acuña Valley, rocky hills in open sun, cover type creosote, *Supernaugh 2 Jan 1951* (lectotype of *E. acunensis*, DES; isolectotype, ORPI) Growler Mts foothills, S of Dripping Springs, 300 ft, 16 Apr 1952, *Parker 7983*. Acuña Valley, *Johnson 2 April 1989* (ASU)

Stenocereus

This genus includes 24 species of columnar cacti; southern Arizona to Honduras, West Indies, and northern South America.

Stenocereus thurberi (Engelmann) Buxbaum

[*Cereus thurberi* Engelmann. *Lemaireocereus thurberi* (Engelmann) Britton & Rose]

Organ pipe; *pitaya*, *pitaya dulce*; cucuvis. (Figure 39).

This stately cactus is the emblem for Organ Pipe Cactus National Monument. Multiple-stemmed, columnar cactus often 2.5–4+ m tall, the branches mostly arising from the base or near the base of the plant, and also often with some branching from the upper stems largely resulting from new growth from freeze-killed stem tips. Stems essentially homomorphic—lower and upper portions of stems similar (in contrast to *Carnegiea* and *Lophocereus*): stems 9–15.5 cm diameter at mid-stem height with ribs of low relief, (14) 15–17 (19) in number, or juvenile plants often with 12–14 ribs. Spines slender, spreading in all directions, longer spines 1–4 (5) cm, straight and needle-like (or occasionally a few spines are twisted); spines bright red as they emerge, quickly becoming dark and then ashy gray to nearly black—young areoles with dark red-brown glandular hairs, producing reddish-brown exudate that often coats the spines and becomes blackish within 1 or 2 years.

Flowers nocturnal, mostly May to July, sometimes flowering through August; flowers 7–9 × 6–7 cm, nocturnal, closing in the early morning; inner tepals white or pale pinkish lavender with

white margins and bases; outer tepals and scales on the floral tube purplish red; nectar chamber relatively large and producing copious nectar. Stamens, style, and stigma creamy white. Fruits globose, 4–6.5 cm diameter, very succulent, indehiscent or splitting irregularly; pericarpel (skin and cortex) thin, red when ripe; floral remnant persistent. Occasional plants have golden-colored spines and produce yellow-spined fruits with yellowish pulp. Unripe fruits green and spiny, the spines lengthening before ripening; areoles readily fall away from the mature fruits, each fruiting areole with 18–32 spines emerging from a dense tuft of short, ribbon-like white hairs, the larger spines often 17–22 mm long, stout (0.4–0.65 mm diameter), usually slightly twisted, stiff, and grayish. Seeds 2–2.5 × 1.4–1.7 mm, blackish, with a weakly developed ridge along the "back." Fruit production (ripening) peaking in July and early August, and sometimes a minor fruiting peak again in September. Fruit pulp, seeds, and rind edible and delicious.

Widespread and common in Organ Pipe on rocky slopes, less common on gravelly bajadas and sandy flats, and on the east side of Cabeza Prieta mostly on granitic slopes and especially common in the Agua Dulce Mountains. In the Ajo Mountains it extends to about 4000 feet where it generally grows with *Juniperus arizonicus* and nestled among south- or west-facing rocks. The midden records probably reflect its arrival in the flora region about 3500 to 4000 years ago, at the beginning of the late Holocene, marking the formation of the modern Sonoran Desert plant communities.

Northern Sinaloa, southwestern Chihuahua, and most of Sonora to south-central Arizona, many Gulf of California islands, Baja California Sur, and southern Baja California.

The basal branching habit of the northern populations is apparently an adaptation to drought. Proceeding southward in Mexico the plants tend to branch higher off the ground, and south and southeast of the Sonoran Desert organ pipes are often arborescent with one or more trunks, and the plants are much larger than in the north. Conspicuous constrictions (scars), common on the stems among the northern populations, are the result of freeze damage and perhaps also drought (e.g., Parker 1987). The stem tip, where the surface-to-volume ratio is highest, is the part most vulnerable to freeze damage. The northern distribution is limited by freezing temperatures and the northwestern limits determined by aridity and more specifically by a paucity of summer rains.

In the thornscrub and tropical deciduous forest south and southeast of the Sonoran Desert in Sonora the organ pipes form well-developed trunks, branching occurs well above the ground, and the plants reach much greater heights than those farther north. Where vegetation is dense, as in the southern portion of the range in tropical deciduous forest, there may be an advantage in having the flowering stems above the forest canopy where they are accessible to bats for pollination and seed dispersal. Proceeding northward into the desert, the plants are progressively shorter until in the northernmost populations, such as in flora area, these cacti are trunkless and the branches arise at or near the base.

Pollination occurs during the night, probably primarily by the nectar-feeding lesser long-nosed bat (*Leptonycteris yerbabuenae*) and if open during daylight hours then primarily by the white-winged dove (e.g., Fleming et al. 1996). The long-nosed bat also feeds on the fruits and is a major seed disperser, and the cave floors of maternal roosts have thick deposits of organ pipe and saguaro seeds. The fruits are also consumed by birds (especially the white-winged dove), ants, and desert bighorn. Packrats (*Neotoma*) often create their middens around the bases of organ pipes, which provide protection and a ready source of food.

In Mexico the plant is known as *pitahaya* (*pitaya*). Some people, especially scholars, say that the plant should be called *pitahayo* (*pitayo*) and the fruit *pitahaya* (*pitaya*) (Santamaria 2000). In practice in Sonora, however, the feminine is in common use. In northwestern Mexico the woody

Figure 39. *Stenocereus thurberi*. Alamo Canyon, Ajo Mts. (A) Mouth of canyon, 9 Sep 2013; (C) 7 Apr 2005. Chuckwalla Hills. (B) 25 May 2006, (F) stem cross section of a fallen plant, 11 Feb 2009. (D) Young spines at stem tip, Organ Pipe plant nursery, 7 May 2006. (E) Estes Canyon, Ajo Mts, 25 May 2005. (G) Ripe fruit, W of Diablo Mts, Ajo Mt Drive, 2 Aug 2013

stem ribs have served for house construction and fences, utensils, and many other utilitarian purposes. The Gachado Line Camp, a restored one room adobe building along the international border about 2 mi E of Lukeville (Broyles et al. 2007: 619), is the only known surviving example of organ pipe wood used in house construction north of Mexico. "A unique feature of the building is its ceiling and roof. Supported by cross beams and vigas, the roof consists of a layer of organ pipe cactus rib poles crossed by a layer of saguaro ribs. Over the saguaro ribs was placed a layer of cardboard, followed by one of creosote bush, then a layer of earth and blacktop" (National Park Service 2008).

Organ pipe fruits are highly esteemed by Sonoran Desert people and the fruit is commercially wild-harvested in southern Sonora and the fresh fruits sold in local markets (Yetman 2006). Unlike fruits of other columnar cacti in the Sonoran Desert region, the rind is relatively thin and edible, and the small seeds are edible along with the fruit pulp (Castetter & Bell 1937; Felger & Moser 1985; Felger et al. 1992). The fruit pulp was eaten fresh and also dried, or made into syrup and jam, and was especially relished for wine (Childs 1954; Felger & Moser 1985; Hodgson 2001; Betty Melvin in Zepeda 1985: 55). Just as they did for the saguaro fruit harvest, the Hia C'ed O'odham seasonally moved their residence for the harvest. Where numerous enough, organ pipe replaced saguaro fruit for ceremonial wine since it is sweeter, juicier, and tastes better. Lumholtz (1912: 331) reported that they "used to come as far as Quitovaquito and Santo Domingo to gather mezquite beans ... and eat sahuaro and pitahaya." Hia Ced O'odham "would collect the fruit of the organ pipe, and they would turn it into jam or else just dry it and eat it, eat it almost like candy" (Betty Melvin in Zepeda 1985: 55). The fruit continues to be a major wild harvested crop for Sonoran O'odham at Quitovac. The Presidential Proclamation establishing Organ Pipe Cactus National Monument in 1937 specifically allows the O'odham to continue their traditional harvest of fruits of the organ pipe cactus and other cacti

OP: Cipriano Well, *Nichol 28 Apr 1939* (ORPI). 1 mi E of Bates Well, 1000 ft, 4 Mar 1940, *Benson 9900*. Quitobaquito, 14 Sep 1974, *Hodgson 14* (ASU). 2.4 mi W of AZ Hwy 85 on Puerto Blanco Drive, 2 mi NW of Lukeville, 19 Jun 1989, *Felger 89-221* (DES). 1.5 km S of Diablo Mountains, Ajo Mountain Drive, 13 May 1990, *Baker 7830* (ASU). 2.5 mi W of Hwy 85 on S Puerto Blanco Drive, 1500 ft, fruits with yellow spines, 11 Aug 1990, *Felger 90-402B*. †Puerto Blanco Mts, on ridge, seeds, modern (30) to 3480 ybp (11 samples).

CP: Ricks' Mine (Simmons 1965: photo, 2 June 1963). Agua Dulce Pass, 14 Sep 1992, *Felger* (observation)

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TRIFOLIUM LAPPACEUM (FABACEAE): NEW TO OKLAHOMA WITH COMMENTS ON THE SPECIES IN TEXAS

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ABSTRACT

Trifolium lappaceum is reported new in Oklahoma. On 11 June 2014 it was collected in Idabel, McCurtain County, Oklahoma, where it was naturalized on both highly disturbed and relatively undisturbed blackland prairie grassland near the entrance to the McCurtain County Regional Airport. Its status using the Fundamental Invasiveness Index of Nesom (2009) is discussed for both the Oklahoma site and the eastern edge of north-central Texas, with the suggestion that it is now likely more common in both north-central Texas and Oklahoma than is currently realized.

Trifolium lappaceum L., lappa clover or burdock clover, is found natively in Mediterranean Eurasia and Africa (Isely 1998). It is one of several non-native *Trifolium* species that are conquering the southeastern USA. It is an annual that is easily distinguished from all other introduced clovers in the region by the 20-ribbed glabrous calyx lobes that have pilose tips (Isely 1998). The common name comes from the bur-like appearance of the fruiting heads.

In the USA there are records from every state in the Deep South (south of the 37th parallel) except Oklahoma and Georgia. Additionally, California, Pennsylvania, and New Jersey now host the species (BONAP 2013). This collection adds Oklahoma to the list of states now known to harbor the species as well.

Voucher. **Oklahoma**. McCurtain Co.: W of Hwy 70 N of entrance to McCurtain County Airport, especially abundant along intermittent drainage and culvert 300 feet N of entrance, 33° 54' 41.25" N, 94° 51' 08.30"W, 11 Jun 2014, *M. White s.n.* (BAYLU).

At this site, *Trifolium lappaceum* was a frequent component of the roadside vegetation as well as highly disturbed grassland west of Hwy 70 (on airport property). It was particularly common along a small sunny drainage 300 yards north of the entrance to the airport. Associate species included weedy species *Bromus japonicus*, *Sorgum halpense, Trifolium campestre* and *Toxicodendron* sp., as well as *Rudbeckia hirta* and *Centaurea americana*. Immediately east of Hwy 70 in the more undisturbed grassland it was found to be an infrequent associate with *Dalea compacta* var. *compacta*, *Manfreda virginica* subsp. *virginica*, *Clinopodium arkansana*, *Rudbeckia missouriensis*, *Castilleja purpurea*, and *C. indivisa*. Using the "Fundamental Invasiveness Index" developed by Nesom (2009), at least locally, it would be currently ranked F2 because it was abundant and widespread in disturbed sites but less common in natural habitats. However, the mowing regime at the site is sure to spread the species and it has the potential to become an F1 invasive even in the undisturbed parts of this site. Additional fieldwork in Oklahoma will be necessary to determine how widespread it has become regionally or statewide.

In adjacent Texas it was first reported by Brown and Peterson (1984) based on collections from two southeast Texas counties—Harris and Hardin—both in May 1979. Turner et al (2003) did not map the Hardin location but added three additional nearby counties—Chambers, Liberty, and Walker. Keith (2013) called it a "rapidly spreading naturalized species" but offered no additional localities.

Two additional collections reported by Carr (1994), from Camp Maxey in Lamar County near the Red River, established the species as disjunct in north-central Texas and were the source of the inclusion in Diggs et al (1999); however in the interim no additional county records have been reported from this area (BONAP 2013). In 2013 it was found to be extremely common at Camp Maxey, but only along mowed roadways, and was growing with another invasive clover, *T. arvense* (pers. obs.). That year it was also discovered as a lawn weed in the author's yard and locally along area roadsides at Campbell, Hunt County, on the extreme eastern edge of north-central Texas but was only photographed, not collected. In 2014, though, the population there was noted to have "exploded," with the species now found extensively along local roadsides as well as in grazed pastures (pers. obs.). In Texas, Nesom (2009) assigned the species a Fundamental Invasiveness Index rating of F3, which meant the species generally occurs in small numbers or is known from typically from only a few disturbed sites. Personal observations of the species from eastern Hunt County would now support the ranking of F2.

Figure 1. *Trifolium lappaceum*, close up of flowering head. Idabel, Oklahoma, 11 June 2014.

Unlike several other introduced species of *Trifolium* (i.e., *T. vesiculosum*, *T. incarnatum*, *T. resupinatum*, and *T. pratense*), which have large or colorful and conspicuous flowering heads that are easily spotted alongside the roadside even from a fast-moving vehicle, the small white flowers and flowering heads of *T. lappaceum* are much more inconspicuous and do not draw attention. Thus it is likely this species is more widely distributed in northern Texas and Oklahoma than is known at the present time. Additional records should be sought elsewhere in both states.

Figure 2. *Trifolium lappaceum*. Idabel Oklahoma, 11 June 2014. Left: detail of flowering head and upper cauline leaves. Right: detail of fruiting head and upper cauline leaves.

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Rodríguez, D. 2014. *Bulbostylis paradoxa* (Cyperaceae), nuevo registro para la flora de El Salvador. Phytoneuron 2014-71: 1–3. Published 1 July 2014. ISSN 2153 733X

BULBOSTYLIS PARADOXA (CYPERACEAE), NUEVO REGISTRO PARA LA FLORA DE EL SALVADOR

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RESUMEN

Se registra la ocurrencia de *Bulbostylis paradoxa* (Spreng.) Lindm. para El Salvador. Se agrega una descripción breve de la especie, fotografías y un mapa que muestra la distribución en el país. En la actualidad solo 6 especies de *Bulbostylis* se conocen para El Salvador.

ABSTRACT

Bulbostylis paradoxa (Spreng.) Lindm. Is reported from El Salvador. A brief description of the species, photographs and a map showing the distribution in the country are provided. At present, only six species of *Bulbostylis* are known from El Salvador.

Adams (1994) en Flora Mesoamericana resume el género *Bulbostylis* y manifiesta que 11 especies del género *Bulbostylis* pueden encontrarse en la región de Mesoamérica. La exploraciones de campo realizadas por el personal del herbario LAGU en la zona oriental de El Salvador, durante los años 2003, 2004, 2005, 2011 y 2014, dejan como resultado el encuentro de *Bulbostylis paradoxa*, ocurriendo hasta la fecha solo en la parte norte del departamento de Morazán y como registro nuevo para la flora del país.

La publicación del registro de la especie no fue posible en los años anteriores a 2014, por no contar con fotografías del espécimen con fenología activa, fue hasta esta última fecha que se logró encontrar la especie en perfecta floración.

Para la identificación de las muestras, se realizó una revisión de literatura de la familia Cyperaceae, en especial del género *Bulbostylis* (Adams 1994; Goméz-Laurito 2003; Kral 2001; Standley & Steyermark 1958) y comparación del material botánico en los herbarios ITIC, LAGU, y MHES.

BULBOSTYLIS PARADOXA (Spreng.) Lindm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26(Afd. 3, 9): 17. 1900. *Schoenus paradoxus* Spreng., Syst. Veg. 1: 190. 1824.

Hierbas perennes. **Tallos**, incluyendo a una masa densa de bases foliares viejas y vainas, 5–12(–20) x 4–5 cm, simples o escasamente ramificados, casi siempre carbonizados. **Hojas** numerosas recurvadas con menos de 0.5 mm de ancho, tan largas o más que los escapos floríferos, filiformes, lisas o un poco escábridas; vainas foliares pardo oscuro, acostillado nervadas, escarioso hialinas y densamente lanoso fimbriadas. **Escapos** 5–23 cm, 1 o varios de cada cáudice, más gruesos que las láminas foliares, erectos, estriados, glabros o híspidos. **Espiguilla** 6–11 x 3–5 mm, solitaria, elipsoide u ovoide. **Brácteas** tan largas como la espiguilla o más largas que ella, aristadas, patentes. **Glumas** 5–8 x 1–1.5 mm, lanceoladas, la costilla media verdosa, excurrente como un mucrón largo, los lados pajizos, pardos o con un matiz rojizo, los márgenes lanoso fimbriados. **Estambres** 3. **Aquenios** 1.5 x 1 mm, obovoides a piriformes, trígonos, los ángulos redondeados más pálidos y más lisos, las caras transversalmente rugulosas; tubérculo deprimido y globoso. Figure 1.

Distribución y hábitat. S. México a Venezuela y Bolivia, Cuba. En El Salvador se encuentra en vegetación de tipo bosque tropical semideciduo mixto submontano, en suelos bien drenados de cenizas volcánicas (MARN 2011), a una elevación de 1134 m.s.n.m. Figure 2.

Discusión. Aunque la distribución de la especie es amplia, en El Salvador la especie solo se encuentra abundante en la zona Oriental, específicamente, en la parte norte de departamento de Morazán. Hasta la fecha la especie se ha reportado, casi para todos los países la región Centroamericana, excepto Guatemala y El Salvador.

Material examinado. EL SALVADOR. Morazán. Mpio. de Arambala, Cantón Cumaro, A.P. Río Sapo, camino a Piedra X, 15 Oct 2003, *Carballo & Monterrosa 00971* (LAGU); Cuenca Río Talchiga 10 Mar 2004, *Carballo, Chicas, & Amaya 01116* (LAGU); Sector Poza La Culebra, 20 Jan 2005 (frt), *Carballo & Monterrosa 02170* (LAGU); Mpio. de Joateca, Caserio El Tizate, A.N.P. La Ermita, Sendero Piedra Pacha-Quebrada El Zope, 14 Jun 2011, *Rodríguez, Monterrosa, Argueta, & Ramos 02382* (LAGU); Sendero hacia Mirador del Borrego, 6 May 2014 (flr, frt), *Rodríguez, Galán, Ramos, & Pereira 04794* (B, K, LAGU, MO); Plan del Borrego, 6 May 2014 (frt) *Galán, Rodríguez, Ramos, & Pereira 02875* (LAGU, MO, NY).

Figura 1. *Bulbostylis paradoxa* (*Rodríguez et al. 04794*). A. Hábitat. B. Espiguillas con flores.

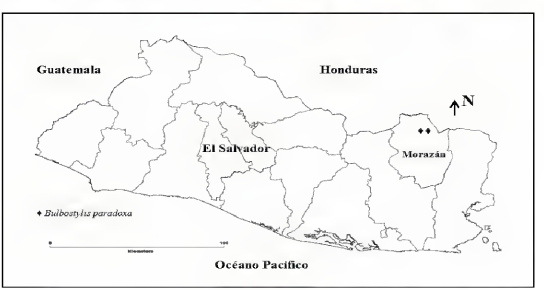

Figura 2. Sitios de recolección de *Bulbostylis paradoxa* en El Salvador.

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Nesom, G.L. 2014. Commentary: Speciation on a local geographic scale in *Mimulus*. Phytoneuron 2014-72: 1–4. Published 14 July 2014. ISSN 2153 733X

COMMENTARY: SPECIATION ON A LOCAL GEOGRAPHIC SCALE IN *MIMULUS*

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Erythranthe (Mimulus) *filicifolia* was recently recognized and formally described as a new species of sect. *Simiola* from Butte and Plumas counties in north-central California (Sexton et al. 2013; transferred to *Erythranthe* by Nesom 2013b). Sexton et al. compared the new species to *E. lacinitata*, as both species have a Sierra Nevadan geographic range, generally similar habitats, and dissected leaves. A closely following companion study (Ferris et al. 2014) sought the evolutionary derivation of *E. filicifolia* among *E. lacinitata* and two other species of sect. *Simiola*: *E. guttata* (in the broadest sense) and *E. nasuta*. Sequence data for 47 of the total 52 "M. guttatus" populations analyzed by Ferris et al. are from two previously published studies: Sweigart and Willis (2003) and Modliszewski and Willis (2012). The M&W study dealt primarily with annuals, but some perennials were represented (Jen Modliszewski, pers. comm.) — which durations might be included in the Ferris et al. analysis is not explicit and apparently impossible for a reader to determine. Only perennials were represented in the CYCA locus study by Ferris et al. (Jen Modliszewski, pers. comm.) — four of these samples (DUN, LMC, PTR, SIM, as inferred from the S&W data) represent the perennial species *E. grandis*; the rest presumably are *E. guttata* in the strict sense (i.e., rhizomatous, perennial).

To investigate degrees of genetic similarity among the four species, Ferris et al. used clustering via PCA for sequence data and maximum likelihood gene trees for each of seven nuclear loci. On the gene trees, *Erythranthe filicifolia* is positioned completely outside of the other three species as a group; on each of the PCA plots, *E. filicifolia* also is isolated. They concluded (p. 10) that *E. filicifolia* is not closely related to *E. lacinitata*, thus it most likely "arose as a completely independent lobed-leaved rock outcrop specialist from some other species like the wide-ranging *M. guttatus*." Because they "were able to only include four species in this analysis, it is not possible to determine its closest relative from our current data." What prevented them from broadening the study's scope is not specified, but a reasonable speculation is that time was allowed only for the original design, which was based on the over-simple assumption that the closest relative of *E. filicifolia* would be among the three species chosen for analysis. It is suggested here that inclusion of only one other species (*E. nudata*), represented by previously published sequence data (e.g., Sweigart & Willis 2003), could easily have been accomodated and would have provided a basis for a more pertinent report.

In the description of *Erythranthe percaulis* (Nesom 2013a) and in making the nomenclatural transfer of *Mimulus filicifolia* to *Erythranthe* (Nesom 2013b, prior to publication of Ferris et al. 2014 and without knowledge of their results), I hypothesized that *E. filicifolia* was probably most closely related to *E. nudata* and *E. percaulis*, both of which also are narrow endemics in the same region as *E. filicifolia*. All three species are annual in duration, completely glabrous to glabrate, and have slightly succulent leaves with prominently reduced surface area. Corollas of *E. nudata* are chasmogamous and allogamous; those of *E. percaulis* and *E. filicifolia* are chasmogamous but very small and probably primarily autogamous (confirmed for *E. filicifolia* by Ferris et al.). *Erythranthe nudata* and *E. percaulis* are restricted to serpentine, while *E. filicifolia* grows mostly on granite outcrops. Of this trio, *E. nudata* and *E. percaulis* are more similar between themselves in overall morphology and habitat and are likely to have a sister relationship. *Erythranthe filicifolia*, in the hypothesis here, is sister to *E. nudata*/*E. percaulis*; an immediate ancestor to this clade may no longer be extant.

With no clear idea of what species *Erythranthe filicifolia* is closely related to and, thus, with no notion of how it might have arisen, one might expect that any related discussion of 'speciation' and 'evolution' would hardly be justified, yet such is the central focus of how the Ferris et al. paper is

advertised (i.e., its title, introduction, a significant part of the discussion, and its conclusion). The rationale that *E. filicifolia* evolved through "local speciation" comes down to simply this (p. 10): "The narrow geographic range of [*E. filicifolia*] compared with other members of the *M. guttatus* species complex from which it might be derived is consistent with it being a product of local speciation." Presumably the phrase "members of the *M. guttatus* species complex from which it might be derived" refers neither to *E. guttata* nor *E. nasuta* (nor *E. grandis*).

Ferris et al. note that "it is not known whether *Mimulus filicifolius* is genetically distinct and/or reproductively isolated from *M. laciniatus*, or whether it is simply a morphologically divergent variety" (p. 2). [Had they found lack of genetic distinction or reproductive isolation, would they then have disavowed recognition of *M. filicifolius* at species rank? Does geographical disjunction provide reproductive isolation? Does distinct morphology imply genetic distinction? Presumably these questions were at least intuitively considered in the initial assessment of Sexton et al.] In seeking a more complete knowledge, the "three main questions" of the Ferris et al. study are stated as these: "(i) Does the recently described *M. filicifolius* differ from *M. laciniatus* in ecology, mating system or genome size as well as in morphology? (ii) Is *M. filicifolius* genetically distinct from *M. laciniatus*? (iii) Is *M. filicifolius* reproductively isolated from *M. laciniatus* or other members of the M. guttatus species complex?" These questions, however [which are answered (i) yes, (ii) yes, and (iii) yes], are related to the strength of definition of *M. filicifolius* as a species — the answers contribute little to an understanding of the process of speciation in the particular case of *M. filicifolius*.

In sum, the main points of Ferris et al. (2014) are essentially (1) that in agreement with Sexton et al. (2013), and adding further details of evidence, they conclude that *Erythranthe filicifolia* is a distinct species but that they do not know where its phylogenetic relationships lie, and (2) that because it has a narrow geographic range relative to some other species (*E. guttata*, *E. microphylla*, and *E. grandis* are not pertinent), it is consistent with "speciation on a local geographic scale."

Local speciation

The introduction of Ferris et al. begins with a contrast between vicariant speciation, where an barrier divides a widespread population system and the correspondingly isolated systems diverge evolutionarily, and local speciation, where small populations split off from a large-ranged progenitor species. They note that the highly restricted geographical range of *Erythranthe filicifolia* makes it "an excellent candidate for local speciation." Absence of evidence in support of this model for *E. filicifolia*, however, reduces their analysis to a tautology: If a species has a relatively local geographic range, then it arose through "local speciation." At face value, using the same logic, the corollary of this seems to be that widely distributed species arose through vicariant speciation.

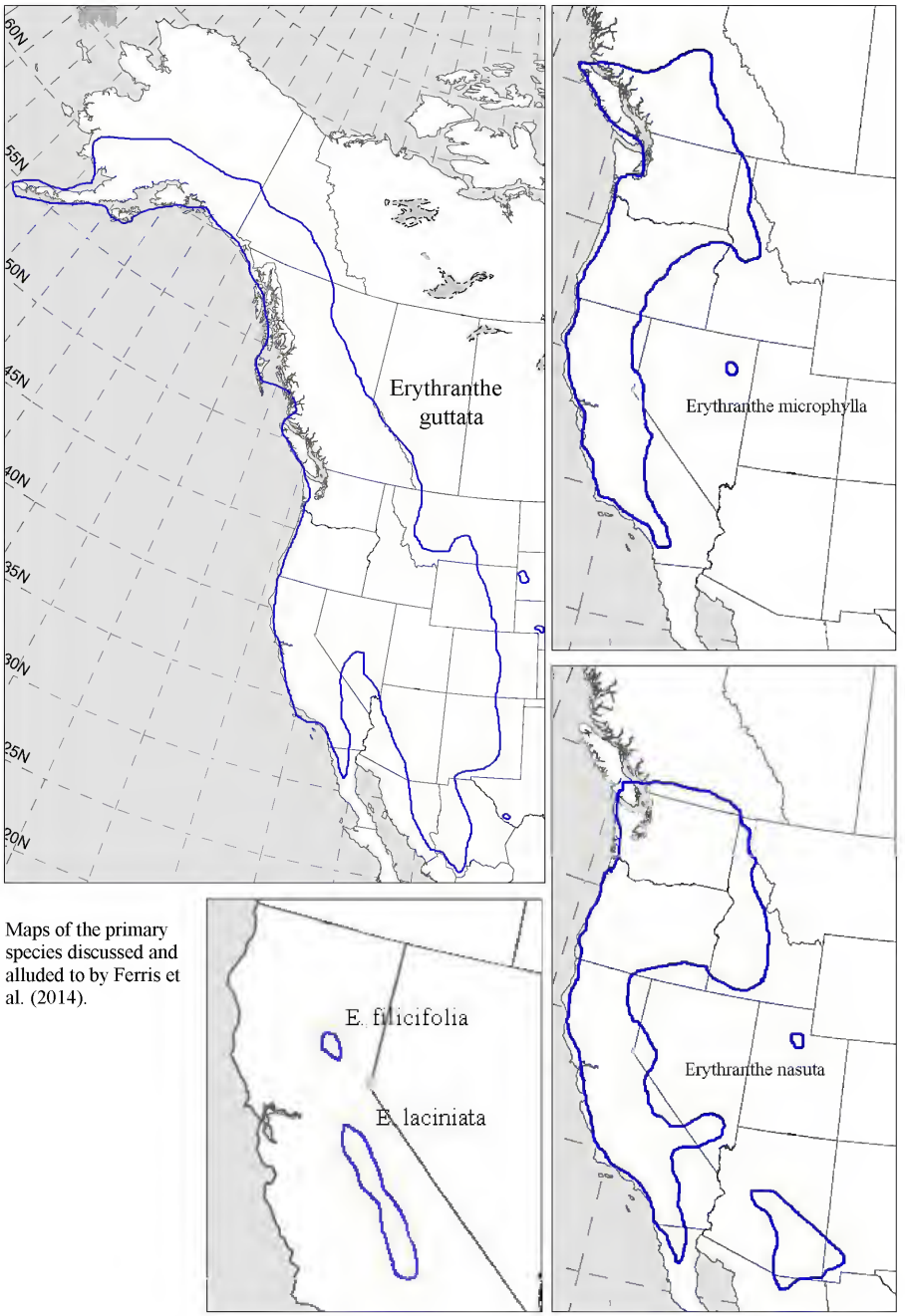
It is entirely possible, without logical or biological constraint, that a species of restricted geography may undergo a vicariant-like event that divides the original population system into two. One of the resultant species might or might not retain the original morphology and biology. Such is what is postulated here for the putative sisters *Erythranthe nudata* and *E. percaulis*.

In anticipation of further discussions of speciation modes that might be similar to that of Ferris et al., here is a geographical accounting of the North American species of *Erythranthe* sect. *Simiola*. The division into three size classes is arbitrary but nonetheless generally indicative of the range of variation. Maps in Nesom & Fraga (2014) provide the bases for these size class assessments.

Narrowly distributed species (1–6 counties or municipios)
arenicola, brachystylis, charlestonensis, chinatiensis, filicifolia, glaucescens, lagunensis, marmorata, michiganensis, nudata, pardalis, percaulis, regni, scouleri, thermalis, visibilis

Moderately distributed species (7–20 counties or municipios)
brevinasuta, caespitosa, corallina, hallii, inamoena, laciniata, minor, parvula, pennellii

Widely distributed species (21 to 100's of counties or municipios)
arvensis, calciphila, cordata, decora, dentiloba, geyeri, glabrata, grandis, guttata, madrensis, microphylla, nasuta, pallens, tilingii, unimaculata, utahensis



Maps of the primary species discussed and alluded to by Ferris et al. (2014).

***Erythranthe guttata* as an ancestral species**

"Because of its wide geographical range and high levels of intraspecific genetic diversity it is likely that *Mimulus guttatus* is the progenitor of the other self-fertilizing species with restricted ranges. This makes the *M. guttatus* species complex excellent for the study of the genetics of recent and local geographical speciation" (Ferris et al., p. 9). Response: an assumption that *E. guttata* is the progenitor of "the other self-fertilizing species [of sect. *Simiola*] with restricted ranges" is ad hoc, with zero underlying evidence. Equally plausible is this statement: *Erythranthe guttata* has spread into a wide geographical range as a result of high levels of intraspecific genetic diversity acquired, via hybridization, from genomic elements of other species. And this: *Erythranthe guttata* and *E. microphylla* are closely related species (but not sister or progenitor-derivative) with considerable gene flow between them, resulting in high levels of intraspecific genetic diversity — *E. guttata* has spread into a relatively wider geographical range because of its ability to reproduce asexually. Etc. Of course, the Ferris et al. assumption may prove to be correct when a species-level phylogeny is objectively documented, but I am aware of many widespread and variable species, over many different genera and families, that are unlikely to be ancestral within their group of close relatives.

As noted above, "*Mimulus guttatus*" in the Ferris et al. study refers to plants that are annual in duration (i.e., *Erythranthe microphylla*) as well as perennial (mostly *E. guttata* but also *E. grandis*). In contrast, the crude map in Figure 1 of Ferris et al. (which gives no indication of how those distributions were determined) apparently is intended to depict the range of the rhizomatous form, i.e., *E. guttata* in the strict sense, or at least to include it (the map also can be construed to include *E. grandis* within the range of *Mimulus guttatus*). Maps 1–4 above are derived directly from county-level distributions developed from revisionary studies of sect. *Simiola* (Nesom 2012, and follow-up studies). The range of *E. guttata* encompasses all of the others (it covers about 3 times the area of that of *E. microphylla*); from mid British Columbia northward, diploids and tetraploids occur in sympatry. The ranges of *E. microphylla* and *E. nasuta* are similar but *E. nasuta* has a greater areal extent and ranges more widely in the southwestern USA, while *E. microphylla* extends further north into British Columbia; *E. filicifolia* is a narrow endemic; *E. laciniata* has a moderate distribution (in the sense above).

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ASSESSING QUALITY OF A REGENERATED PRAIRIE USING FLORAL AND FAUNAL INDICES

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ABSTRACT

In today's highly fragmented landscape, prairie communities are becoming rarer as they give way to woody species encroachment, land development and agriculture. In response to this loss, many prairie restorations have taken place implementing seeding, planting and a number of management techniques. However, there is a possibility that natural successional processes may result in quality prairie communities. The goal of the present study was to determine the quality of a late successional prairie located in Macoupin County by its resemblance to several restored and remnant prairies. It was hypothesized that the site would have low floristic quality since no restoration or management practices have been routinely implemented. Vegetation cover data were collected in early and late summer of 2011 and 2012. Species richness (*S*), antilog of Shannon diversity (N_1), average coefficient of conservatism (*mean C*) and Floristic Quality Index (*FQI*) were calculated for each sampling season. These were also calculated for a comprehensive species list from the study site and four sites of known quality for comparison (N_1 was not included in these calculations due to a lack of abundance data). Bray-Curtis dissimilarities between sites were also calculated based on the species composition of these sites. Auchenorrhyncha (Insects: Hemiptera) were collected on four 40 m transects within the site. Auchenorrhyncha Quality Index (*AQI*), *S*, N_1 and *mean C* were calculated based on count data from these transects and others located in eight comparison sites. Indicator species were also found for the study site and each comparison site. Analysis of the abundance data showed that from 2011 to 2012 there was a decline in all four diversity index scores, likely due to drought. Comparisons between the study site and other high quality restorations and remnants revealed that the site does indeed have high floristic integrity, contrary to the hypothesis, though it was not very similar to any of the other sites in species composition. Results from the Auchenorrhyncha survey were consistent with those of the vegetation survey. When compared with those of other high quality sites, diversity index scores from the study site were all very similar and in some cases higher. This, again, was contrary to the hypothesis. Indicator species analysis revealed that the study site supported lower quality species than comparison sites.

It is estimated that prior to European settlement and the establishment of agricultural practices prairies, plant communities comprised mainly of grasses, forbs and some shrubs, covered more than 68 million hectares within the Great Plains (Robertson et al. 1997). Part of this area extended eastward covering parts of Iowa, Missouri, Indiana and Illinois to form the Prairie Peninsula. Due to a combination of geography, topography, glacial history, climate, and fire frequency, Illinois was dominated by this prairie while in other parts of the peninsula it existed as a mosaic of prairie and forest (King 1981; Brugam & Patterson 1996). In today's highly fragmented landscape, prairie communities are becoming rarer as they give way to woody encroachment, land development and agriculture. Illinois now retains less than 0.01% of its original prairie habitat and many of these remnants have been reduced to small, widely spaced inclusions surrounded by woodland (Brand & Dunn 1998; McClain et al. 2002). This loss has led to attempts at prairie restorations, all of which have the similar goal of reestablishing native plant species via plantings or seeding and different management techniques such as controlled burning (Camill et al. 2004). A

number of these reconstructions have been successful, however, it has been demonstrated that species diversity in these sites can decline over a period of time, even with continued management (Kindscher & Tieszen 1998). In contrast, other studies have shown that there is a possibility for natural successional processes to result in quality prairie communities (Edgin & Ebinger 2000). The present study was an attempt to determine the resemblance of an old, wet-mesic field in late stages of succession to a prairie remnant using floral and faunal quality indices.

History of restoration

Although preservation of natural areas began as early as 1919, restoration of natural areas did not become a concern until the 1930s when ecologists realized that the majority of tallgrass prairie once occurring in the prairie peninsula had been converted to agricultural fields (Smith 1998). This realization spurred plantings throughout the Midwest, beginning with Curtis Prairie in Wisconsin, which is the world's oldest prairie restoration (Jordan 1983). Since the 1930s many restorations have taken place, most with the final goal of replicating the area's historic ecosystem (Allison 2002). This goal is a difficult one to reach as many sites do not have a history complete with quantitative data on species that were present (Westman 1991). It has also been criticized for being one-dimensional as restoration ecologists tend to focus solely on vegetation, ignoring faunal ecosystem elements (Betz 1986). In recent years, a number of studies have been conducted to determine how restoration practices affect prairie fauna including insects (Brand & Dunn 1998; Panzer 2002), birds (Herkert 1994), and small mammals (Diffendorfer et al. 1995). These are all steps in the right direction, but there is still much work to be done in understanding how to make restorations successful.

Success of a restoration is dependent upon the goals set by the manager prior to restoration taking place. As stated before, the most common goal for restorations is to return a site to its historic state, which is difficult due to lack of information (Westman 1991; Allison 2002). As a result, restoration managers turn to remnant prairies as guides and try to replicate them as closely as possible (Schramm 1990). This still is a hard goal to achieve since no two remnants are exactly alike and no ecosystem is capable of remaining void of change over time (Howell and Jordan 1991). The Society of Ecological Restoration (2004) outlined a number of criteria to be met for successful restorations, including species composition similar to that of a reference system, existence of necessary functional groups, and resilience in the face of normal stressors. Some of these criteria are difficult to measure and not all factors of ecosystem function can be assessed within temporal and monetary constraints, but these should be considered when outlining the goals of a restoration (Society of Ecological Restoration 2004).

In recent years, ecologists and restoration managers have attempted to quantify restoration success using a number of measurements. Some suggest using measurements such as proportion of native species, net primary productivity, and plant and animal diversity as indicators of success (Martin et al. 2005). More simple measurements, such as species richness, are used for determining quality, though they are commonly accused of not being truly sensitive to habitat integrity (Bowles & Jones 2006; Taft et al. 2006). Most recently, the Floristic Quality Index, a weighted index that is said to measure biological integrity, has become one of the most widely used measurements of both restoration success and remnant quality, with multiple variations for different regions (Taft et al. 1997; Bowles & Jones 2006).

While plants are considered by many to be among the best biological indicators of habitat integrity (Panzer & Schwartz 2000), some argue that focusing solely on plants can lead to incomplete goals and management strategies, especially within restorations (Pressy et al. 1993; Bomar 2001). Such a narrow scope can have adverse effects on other wildlife populations that take refuge in managed areas, as has been demonstrated in taxa such as birds (Swengel & Swengel 2001), insects (Panzer & Schwartz 2000) and some species of mammals (Erwin & Stasiak 1979). In response to

this, some are turning to animal based assessments to determine habitat quality. Schorr et al. (2007) investigated using survival of rodents as a determinant of xeric habitat quality, though numerous variables made it difficult to produce robust models. Karr (1981) developed an Index of Biological Integrity (IBI) using fish metrics to assess quality of streams in the Midwest, which was found to be sensitive to differences in habitat degradation in a variety of situations (Karr et al. 1986; Leonard & Orth 1986; Karr et al. 1987). In Australia, a similar index was also developed for ants (Majer and Beeston 1986) which are considered to have many characteristics that are useful for monitoring development of restorations (Andersen 1990).

Arthropods have shown themselves to be very useful in the assessment of habitat quality (Kremen et al. 1993). Characteristics including large population numbers, diversity of occupied niches, variety of ecological roles, and quick developmental rates make them particularly good candidates for this use (Longcore 2003). Until recently, difficulties with identification and limited documentation of life histories have prevented widespread use of arthropods as indicators of ecosystem integrity (Andersen & Majer 2004; Dietrich 2009). Wallner (2010) developed an index similar to *FQI* using Auchenorrhyncha, or hoppers (Insects: Hemiptera [DeLong 1948]) called the Auchenorrhyncha Quality Index (*AQI*). This group displays the useful characteristics of most arthropods, with the added attraction of being well documented taxonomically (DeLong 1948). *AQI* uses the same principle as *FQI* of weighting species according to their dependence on natural habitat. Each species is designated a coefficient of conservatism that can range anywhere from zero to 18, and is based on a number of measureable, physical characteristics and life history traits. Although some may subject it to the same criticisms as *FQI*, *AQI* has been statistically validated and in time may prove to be a very useful tool in grassland management (Wallner 2010).

Restoration through succession?

Though major loss of prairie habitat has led to attempts at reconstructions via plantings and invasive management techniques, there is a possibility that natural successional processes may also result in quality prairie communities (Edgin & Ebinger 2000). This means that if a piece of land is left undisturbed, it has some potential to regenerate to a more natural state. This strategy has been observed in a number of different habitats. Galatowitsch and Van der Valk (1996) found that in prairie wetlands succession did not lead to plant communities similar to those of remnant wetlands, though there was evidence that, given time, the similarity could increase. Hodacova and Prach (2003) surveyed spoil heaps left after mining, and found that spontaneous succession favored higher species richness and resulted in dense herb layers that were better suited to prevent erosion than those produced by active restoration. Tropek et al. (2010) studied abandoned limestone quarries and found that the extreme heterogeneity in successional sites provided habitats for many endangered species of vascular plants and arthropods. On the other hand, technical reclamation established sites dominated by fast growing, ruderal species. These are only a few examples and much more research is required to determine whether succession can regularly give rise to more natural landscapes. It is well established that successional processes will occur and must be incorporated into restoration practices for them to be successful (Harker et al. 1997), but it remains to be seen if it can stand alone.

If areas can be left to themselves to regenerate, this may have major implications for future restoration efforts. If there are no concerns that require technical reclamation techniques, succession is a less invasive, cost effective, simple approach for restoration of natural areas (Tropek et al. 2010). These benefits could be used in persuading land owners to allow fallow fields to be incorporated into the natural landscape, rather than developing or leasing them to farmers. If monetary incentives could be linked with these benefits, it is possible that natural area reclamation would not be such a rare and difficult occurrence.

The objective of this study was to determine similarity of an old field in later stages of succession to remnant and restored prairies. Comparisons were made to a number of sites using the following biodiversity variables: species richness (*S*), the antilog of Shannon's diversity index (*N1*), average coefficient of conservatism (*mean C*), the Floristic Quality Index (*FQI*), and the Auchenorrhyncha Quality Index (*AQI*).

Study site

This study was conducted at a site in Macoupin County, Illinois, located 3.4 km ENE of Benld (39.06392° N - 89.45570° W; S28 T8N R6W). The site is a 1.4 ha field surrounded by oak-hickory forest to the south, east and west, and by agricultural fields to the north. The site is located in the Cahokia Creek Watershed and is on the boundary line between two natural divisions of Illinois, the Western Forest-Prairie Division (Carlinville Section) and the Southern Till Plain Division (Effingham Plain Section) (Schwegman1973). The field is dominated by forbs, with scattered grasses and sedges. The current owner purchased the property in 1977, at which point the field was in early stages of secondary succession. Since that time, the site has not undergone plowing or grazing by domestic animals, though it is believed to at one time have been used for agricultural purposes. Since 1986, the site has experienced occasional fires, some spontaneous, some managed, and very little mowing to prevent establishment of trees and shrubs. During the present study, the site was neither mown nor burned.

Soil is in the Marine silt loam series (type number 517B) which is somewhat poorly drained and is derived from parent material of loess over silty pedisediment. Climate of the region in which the site occurs is humid and temperate, with a mean annual temperature of 12.2°C. Total mean annual precipitation is about 980.4 mm, 57% of which falls between April and September.

METHODS AND MATERIALS

Vegetation field methods

A preliminary survey was carried out in 2010 in order to become acquainted with species present in the site. Each species encountered was collected, pressed and identified according to Mohlenbrock (2002), as were all species collected throughout this study. In addition, type specimens of all taxa were brought to the University of Illinois and verified by Paul Marcum and Rick Phillipe of the Illinois Natural History Survey.

Vegetation was surveyed during the 2011 and 2012 growing seasons. Stratified sampling was used to insure that the site was sampled fairly evenly, rather than heavily in a few areas and not at all in others. As such, the site was split into six sections, sections A through F, (Fig. 1) and random plot centers were generated within each section in proportion to the section's size. Constraints on plot placement were that a plot could not be closer than 0.50 m to a boundary line, and that all plots would be separated by ≥0.50 m. In total, 200 plots were generated for the entire site, 102 of which were used in this study (Fig. 2). Plots were located within the site using a handheld GPS (Garmin eTrex Legend, ± 15 m) and were staked and marked with a section letter and number for later relocation.

Sampling plots were 0.25 m^2 quadrats centered on each point Each species found within the square was recorded along with its percent coverage which was based on a modified Daubenmire (1959) coverage class. The classes were as follows: 1, <1; 2, 1-5; 3, 5-25; 4, 25-50; 5, 50-75; 6, 75-90; 7, 90-100 (ranges are percentages of the square). The site was sampled in two successive years (2011 and 2012). Each plot was sampled twice each year, in early summer (June 28 and July 6-7, 2011, and June 4-6, 2012), and late summer (August 23, 25, 30, and September 1 in 2011, and August 25, 26, and 30 in 2012).

Figure 1 Satellite image of study area with surveyed plots shown in white

Vegetation analysis

Both native and non-native vegetation data were used to calculate *S*, *N1*, *mean C*, and *FQI* for the study site. All calculations were done for species found within plots while *S*, *mean C*, and *FQI* were also calculated for the overall species inventory for comparison with inventories acquired from other sites (Table 1). Abundance measures were not available for all sites, thus *N1* was not included in this comparison as it was for the Auchenorrhyncha. Species composition was also used to calculate dissimilarity values between all sites using the Bray-Curtis dissimilarity index (Faith et al. 1987). This was done in the program DECODA (Minchin 1998).

Table 1. Name, status (restoration or remnant) and size (in hectares) of each site used in comparison study. All sites are located in Illinois and status for each (except for study site) was determined by either the Illinois Natural History Survey or the Illinois Natural Area Inventory

Site	Designation	Size (ha)
Study Site	Restoration	1.5
Matanzas	Preserve	11.0
Midwine (South Patrol Road)	Restoration	190.2
Midwine (Exon Mobil Natural Area)	Preserve	15.8
Denby Prairie	Preserve	1.0

Auchenorrhyncha field methods

The layout for insect sampling differed from that for vegetation sampling because the *AQI* calculation was found to be more robust when transects were used rather than plots (Wallner 2010). Sampling took place along four 40 m transects (Fig. 3). Because the study site was long and narrow, transects were set up haphazardly rather than in parallel in order to keep them within the site and reduce edge effects (Wallner 2010). A leaf blower (Ryobi ™, South Pasadena CA) with a netted vacuum attachment was used for collection. The length of each transect was vacuumed for a total of five minutes, which was done at one minute increments to prevent plant material buildup in the collection net. After each minute, contents of the net were transferred to a Photo Tactic Utility Insect Extractor (PTUIE) and left for forty-five minutes to an hour for separation of insects from plant material. All Auchenorrhyncha collected in this fashion were separated and placed into small vials containing 70% ethanol and labeled with transect number and a letter to identify the individual. All specimens were identified to species by Chris Dietrich, systematic entomologist for the Illinois Natural History Survey.

Auchenorrhyncha were sampled on October 5, 2012. It is usually suggested that sampling for Auchenorrhyncha take place during late summer, around July or August (Blocker and Reed 1976). However, development of these insects is closely tied to host plant phenology (Dietrich pers comm.) and a long drought that occurred during the study period delayed plant maturation. On the advice of Chris Dietrich, sampling was carried out later in the year to permit plants and insects to mature.

Analysis of Auchenorrhyncha

Both native and non-native specimens were used to calculate *S*, N_1, and *mean C* (Table 2), as well as the Auchenorrhyncha Quality Index (*AQI*). The coefficients of conservatism for Auchenorrhyncha are, as with plants, indicators of each species' reliance on natural habitat for survival and reproduction, though their range is 0 to18 rather than 0 to 10. The calculation for *AQI* is the same as that for *FQI*.

All four biodiversity variables were calculated for the study site and a number of comparison sites known to be of mid to high quality. Comparison sites were sampled by Adam Wallner (2010) using the same methods described above, only some of the sites used three transects rather than four (Table 2). This comparison is necessary since *AQI* is not yet widely used and therefore does not have a standard rule of thumb for interpreting single scores like *FQI* does (Taft et al. 1997). Transect data were used to create a database in DECODA which was then transferred to PC-ORD (McCune & Mefford 2006) to find indicator species for each site.

Table 2. Name, abbreviation, size, number of transects sampled, and State location of each site used for comparison in Auchenorrhyncha survey. All sites have a designation of mid to high quality according to INAI grades.

Site	Abbreviation	Size (ha)	Number of Transects Sampled	State
Study Site	SS	1.5	4	Il
12 Mile	TM	38.0	4	Il
Cayler	CA	64.7	4	IA
Chloe	CH	61.0	4	MO
Hayden	HP	97.1	4	IA
Faville	FA	24.3	3	WI
Midewin	MI	6070.3	3	IL
Matanzas	MA	11.3	3	IL
Gooselake	GL	242.8	3	IL

RESULTS

Vegetation

Scores in all diversity indices remained fairly stable over the four sampling seasons though a drop occurred in N_1 for both 2012 seasons, as well as in the 2012 late season for *S* and *FQI* (Table 3). *Mean C* scores were consistent over all four sampling seasons. In all four seasons, *FQI* seems to be relatively low and not indicative of a quality area.

Table 3. Diversity variables calculated for the study site over four sampling seasons.

Variable	Sampling Season			
	2011		2012	
	Early	Late	Early	Late
S	79	73	74	61
N_1	25.22	28.04	20.02	20.08
mean C	2.62	2.73	2.59	2.46
FQI	23.29	23.29	22.32	19.21

When indices were calculated for a more comprehensive species list and compared to those for other sites known to be of good quality, scores for all sites were very similar (Tables 4 and 5). An *FQI* of 35 or greater tends to suggest an area of high floristic integrity (Taft 1997). Although *FQI* can be influenced by site size *mean C* is considered an area-independent variable that can readily be used for comparisons.

Table 4. Diversity variables calculated based on comprehensive inventories of the study site and four comparison sites. N_1 was not included as no abundance measures were available for the comparison sites.

Variable	Site Name				
	Study Site	Matanzas	Midewin (SP)	Midewin (EX)	Denby
S	209	150	293	253	149
mean C	2.79	3.39	2.40	2.75	3.13
FQI	40.40	41.56	40.96	43.69	38.26

Table 5. 95% confidence intervals for comparison sites calculated for each variable

Variable	95% CI
S	94.85- 327.65
mean C	2.23- 3.61
FQI	37.56- 44.68

Dissimilarity calculations resulted in high scores among all sites, showing that there is very little similarity among the sites based on species composition (Table 6). The lowest score, i.e. greatest similarity, occurred between the two Midwine sites. This of course is not surprising as they occur very close to one another and likely experience similar management strategies.

Table 6. Bray-Curtis dissimilarities based on species composition of the study site and four comparison sites. High scores correlate to low similarity between two sites.

	Study Site	Matanzas	Midewin (SP)	Midewin (EX)
Matanzas	0.65	-	-	-
Midewin (SP)	0.66	0.67	-	-
Midewin (EX)	0.71	0.68	0.45	-
Denby	0.67	0.60	0.63	0.65

Auchenorrhyncha

As with the vegetation, scores for diversity indices were similar among the study site and comparison sites (Tables 7 and 8). Again these sites are of known quality and have INAI scores between A and B, indicative of high quality natural areas. Unlike FQI, site size is not a problem with the AQI calculations here since they are all based on sampling a limited number of transects.

Table 7. Diversity variables calculated based on transect surveys of the study site and eight comparison sites.

Variable	Site Name								
	Study Site	12 Mile	Cayler	Chloe	Hayden	Faville	Midewin	Matanzas	Gooselake
S	23	26	24	26	30	18	22	24	27
N_1	12.60	16.72	11.52	20.36	9.18	7.04	12.89	15.35	13.30
mean C	7.69	8.39	7.69	6.11	6.52	8.84	8.32	5.99	8.92
AQI	36.87	42.80	37.66	31.18	35.69	37.53	39.07	29.34	46.33

Table 8. 95% confidence intervals for comparison sites calculated for each variable

Variable	95% CI
S	21.63- 27.62
N1	9.76- 16.83
mean C	6.58- 8.62
AQI	32.78- 42.12

Indicator species analysis revealed that while the sites received similar scores for all biodiversity variables, the study site is mostly characterized by hopper species that are less conservative than those that characterize the comparison sites (Table 9).

Discussion

It is difficult to measure the time it takes for plant communities to respond and change when faced with disturbance, in part due to the short time frame in which most field studies occur (Tilman 1982). Adding to the difficulty is the fact that these communities exist in a loose equilibrium, meaning that while there may be high fluctuation in composition and abundance in response to disturbance on a short time scale, structure generally remains stable when viewed on a longer time scale (De Angelis et al. 1985). That being said, no community can remain the same over any period of time even with an apparent lack of disturbance (Collins 2000). Results of the present study concur with the idea that great variation occurs in brief amounts of time. Table 3 summarizes this variation within the study site, showing that even over the course of a single growing season there were changes in species composition and abundance. The change from 2011 to 2012 was even more drastic, with drops occurring in each of the diversity measurements. This was likely due to an extended drought period that occurred during the study. A longer time frame would be necessary to discern whether the diversity and quality would recover to its former state and persist as a stable entity as predicted by the loose equilibrium hypothesis. Although the *FQI* scores seem to be indicative of a low quality area, these scores are likely an artifact of low sampling intensity (plot data vs. species inventory). Thus they merely reflect temporal changes rather than overall site quality.

In comparing the study site to other high quality natural areas, it was surprising to find that it was comparable based on the diversity indices measured (Tables 4 and 5). Although the comparison sites were much larger, in all three diversity indices the study site scored higher than one or more of the comparison sites. Based on the dissimilarities calculated it cannot be said that the study site is very similar to any of the comparison sites (Table 6). This is not surprising as each of the sites occurs in very different areas with varying environmental aspects. Management practices, grazing by herbivores, topography, soil type and many other variables can influence species composition and differences in these variables can lead to areas that look very different (Hartnett et al. 1996). This does not however mean that two areas with different species compositions cannot be of similar quality. Two sites could not share a single species in common and still have the same average coefficient of conservatism (Taft et al. 1997).

The results of this survey beg the question, where did this prairie come from? It was stated earlier that the landowner did not seed or plant the site and that very little was done in the way of management. Seed banks are one possible explanation. Species capable of producing seed banks have evolved mechanisms to prevent premature germination, so seeds will remain dormant but viable until proper conditions are met (van Baalen 1982). Seeds of some species are able to remain viable for very long periods of time, some up to 100 years (Kivilaan & Bandurski 1981). An important aspect of germination of banked seeds is their return to a desirable depth in the surface soil as

Table 9. Auchenorrhyncha indicator species for study site and comparison sites. Each species is shown with corresponding coefficient of conservatism and indicator value. Statistical significance was tested by randomizing group membership 10,000 times. Significant indicators ($P < 0.05$) are listed in descending order of indicator value within each group.

Site	Species	CC	IV	*P*
SS	*Latalus sayii*	5	97.3	0.0002
	Scaphytopius frontalis	4.75	90.9	0.0001
	Masamia sp.	11.875	75.0	0.0038
	Toya propinqua	0	75.0	0.0050
	Scaphytopius acutus	4.75	57.3	0.0203
TM	*Kelisia curvata*	13.25	100.0	0.0001
	Prosapia bicincta	6.25	75.0	0.0051
	Xerophloea peltata	8.5	54.9	0.0145
CA	*Extrusanus orrysus*	12.75	100.0	0.0003
	Commellus comma	11.75	75.0	0.0041
	Scolops sulcipes	11.5	75.0	0.0003
	Diplocolenus configuratus	12	70.0	0.0028
	Athysanus argentarius	0	55.9	0.0001
	Doratura stylata	0	48.2	0.0028
CH	*Bakerella rotundifrons*	10.25	100.0	0.0003
	Stirellus bicolor	6	88.9	0.0003
HA	*Agalliota constricta*	3	94.7	0.0002
	Agalliopsis novella	4.75	75.0	0.0040
	Empoasca fabae	1.5	75.0	0.0050
FA	*Erasmoneura tecta*	10	100.0	0.0009
	Megamelus metazeri	14.5	100.0	0.0009
	Memnonia panzeri	17	100.0	0.0009
	Kelisia pectinata	13.25	76.9	0.0003
	Cicadula melanogaster	9.5	76.3	0.0048
	Caenodelphax nigriscutelleta	13.5	71.4	0.0027
MI	*Flexamia prairiana*	11.75	100.0	0.0010
	Aflexia rubranura	16.5	66.7	0.0244
	Bruchomorpha dorsata	12.25	51.3	0.0255
MA	*Kelisia vesiculata*	9.5	100.0	0.0009
	Amplicephalus osborni	13	66.7	0.0251
	Delphacodes puella	5.5	66.7	0.0251
	Graminella nigrifrons	2.5	66.7	0.0251
	Pissonotus piceus	10	66.7	0.0251
	Forcipata loca	1.5	43.9	0.0321
	Xestocephalus desertorum	4	40.7	0.0417
GL	*Destria fumida*	16	100.0	0.0012
	Deltocephalus gnarus	11.5	66.7	0.0268
	Neohecalus magnificus	15.75	66.7	0.0241
	Opsius stactogalus	0	66.7	0.0268
	Xestocephalus pulicarius	4	64.0	0.0058
	Dorydiella kansana	13.5	49.0	0.0151

opposed to being buried deeply (McRill & Sager 1973; Grant 1983). One would assume that if the site had a history of cultivation, plowing would have brought these seeds up towards the surface and allowed them to germinate, thus exhausting the seed bank over time. However, the history of the site is still under question as no records can be found of its previous use, so the presence and subsequent germination of a seed bank is still a plausible explanation for the source of species present. Another possibility is that seeds were brought in from surrounding sources. In driving around the area, it was noticed that several patches containing the same species found in the site occurred on the outskirts of wooded areas and fields and alongside roads. Though in most cases seeds move only very short distances on their own (Howe & Smallwood 1982) there are circumstances under which they can be dispersed over much greater distances. Birds and large herbivores can serve as vectors for seed dispersal (Collins & Uno 1985). Some species produce fruits that can be transferred via the fur of passing animals. Species in the genus *Desmodium* have flat, sticky fruits that can grasp onto fur, clothing and even bare skin. There are other species that produce seeds with appendages that enable them to remain air-borne for a long period of time. Many species in the family Asteraceae have seeds with a feather-like pappus for wind dispersal. Cain et al. (2000) emphasize the importance of long-distance seed dispersal and the furthering of our understanding of the topic through more experimentation.

Results from the Auchonrrhyncha survey reflect the findings from vegetation surveys. Wallner et al. (2012) found a similar correlation when FQI, AQI and other diversity indices were used to evaluate quality in hill prairie restorations and remnants. All index values used were capable of distinguishing among high, mid and low quality hill prairies.

In the present study, scores for all diversity indices were similar across the study site and all comparison sites, indicating that the study site is comparable in quality to the others (Tables 7 and 8). Because no specific management plans are currently in practice in the study site, it is not known how burning and/or mowing would affect these insects. Some studies have shown that prairie arthropods respond differently to management than plants (Swengel & Swengel 2007). This should be taken into consideration so as to not damage the existing communities. A survey would have to be conducted after the implementation of management practices in order to determine the effects on Auchenorrhyncha as well as an appropriate disturbance regime. Wallner (2010) observed that Auchenorrhyncha populations also corresponded closely to the types of vegetation present. He concluded that presence and abundance of conservative Auchenorrhyncha species was dependent on the presence of perennial C4 grasses, thus management for these species should include maintenance of these grass communities.

Although index scores showed the study site to be similar to the comparison sites, indicator species analysis revealed that not only are the sites characterized by completely different species, but also that the study site is characterized by species with lower conservatism scores than those of the comparison sites (Table 9). In fact, the study site seems to support mostly lower quality species, whereas high quality species are relatively abundant in many of the comparison sites. The inability of quality indices and diversity measurements to detect these types of differences poses a problem for ecologists and restoration managers. Index scores alone could lead one to believe that a natural site is maintaining populations of quality species, or that a restoration is successful, when in fact they may have very low or even decreasing numbers of conservative species. In order to prevent these misconceptions, indicator species analysis should be combined with quality indices and diversity measurements when surveying natural areas (Dufrêne & Legendre 1997).

In conclusion, the results of this study do not support the hypothesis that succession without the aid of management would result in a site with low floristic integrity. In fact, according to all the diversity indices scores the study site has very high floristic integrity. Studies conducted in multiple

habitat types yielded similar results (Edgin & Ebinger 2000; Galatowitsch & Van der Valk 1996) and in some cases succession lead to areas of better quality than those restored mechanically (Hodacova & Prach 2003; Tropek et al. 2010). Of course, success of natural restoration is likely dependent on edaphic aspects of the site itself (e.g. moisture availability, soil nutrients) and the availability of local seed sources (Řehounková & Prach 2007). All sites will not have these attributes, so mechanical restoration and management would still be necessary. Also, eradication and prevention of encroachment by exotic and woody species would still be required over time, as is the case with the study site. Nonetheless, successional processes should be accounted for in any type of restoration attempt to increase the likelihood of success.

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AVICENNIA GERMINANS (ACANTHACEAE) GAINING NEW GROUND IN SOUTHEAST TEXAS?

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ABSTRACT

Avicennia germinans is documented for the first time from Brazoria County in southeast Texas. It perhaps indicates an expanding range for the species in Texas.

Avicennia germinans (L.) L. (black mangrove) is a tropical and subtropical maritime shrub to small tree distributed along tidal shores from Texas to Florida, Bermuda, the Bahama Islands, both coasts of Mexico and Central America, the West Indies, and the coasts of Brazil, Peru, and West Africa (Correll & Johnston 1970; Godfrey & Wooten 1981).

The northern distributional limit of *Avicennia germinans* has been suggested to be determined by the frequency and duration of freezing temperatures (Sherrod & McMillan 1981). In the Gulf of Mexico, *A. germinans* sees its northernmost limit in Texas. Herbarium records occur from the South Texas coastal counties of Aransas, Calhoun, Cameron, Kleberg, Nueces, and San Patricio (Fig. 1) with well established stands at three sites (Sherrod & McMillan 1981). The species does not occur northward again until Galveston and Jefferson (the northernmost limit) counties in southeast Texas (Fig. 1). Although probably a waif in Jefferson County, as reported by Sherrod and McMillan (1981), Guo et al. (2009), and suggested by few herbarium collections, a well established population occurs in tidal marsh adjacent to "The Lagoon" on northeast Galveston Island (Rosen, personal observation). Outside of these two locations, the species is not documented from any others between Jackson County and the Louisiana border in southeast Texas. A specimen at TEX collected by R.J. Fleetwood on Galveston Island in 1973 indicates that "This species occurs on Bird Island, 1.5 mi W of San Luis Pass and the N end of Mud Island between West Bay and Christmas Bay [both in Brazoria Co.]"; however, we have located no herbarium specimens at BRIT, SMU, TEX, TAES, or TAMU for these sites.

Recently, floristic field work at a newly acquired 178.8 ha tract that is part of the Christmas Bay Coastal Preserve on Follets Island has yielded a collection of *Avicennia germinans*, representing the first vouchered record for Brazoria County. The site is ca. 55 kilometers southwest of the population at The Lagoon on northeast Galveston Island.

Voucher specimen. **Texas.** Brazoria Co.: Follets Island; on and N of County Road 257 (Bluewater Highway), about 10 km W of the San Luis Pass bridge, locally rare (a single individual) evergreen shrub to about 0.5 m tall in tidal salt marsh with *Spartina alterniflora*, *Batis maritima*, and *Sarcocornia utahensis,* producing many pneumatophores, 29 Jun 2014, *D.J. Rosen 6581* (TEX), *S. Zamirpour 74* (BRIT; Fig. 2a & b). Two larger shrubs were also seen adjacent to a tidal inlet nearby (Fig. 2c).

Recently, *Avicennia germinans* has been reported to be advancing northward in Louisiana (Perry & Mendelssohn 2009) and expanding in extent in populations in south Texas (Everitt et al. 2010) in response to climate change. We believe our collection reported here may be an indication of the species expanding its distribution in southeast Texas. In any case, black mangrove apparently is rare in Brazoria County.

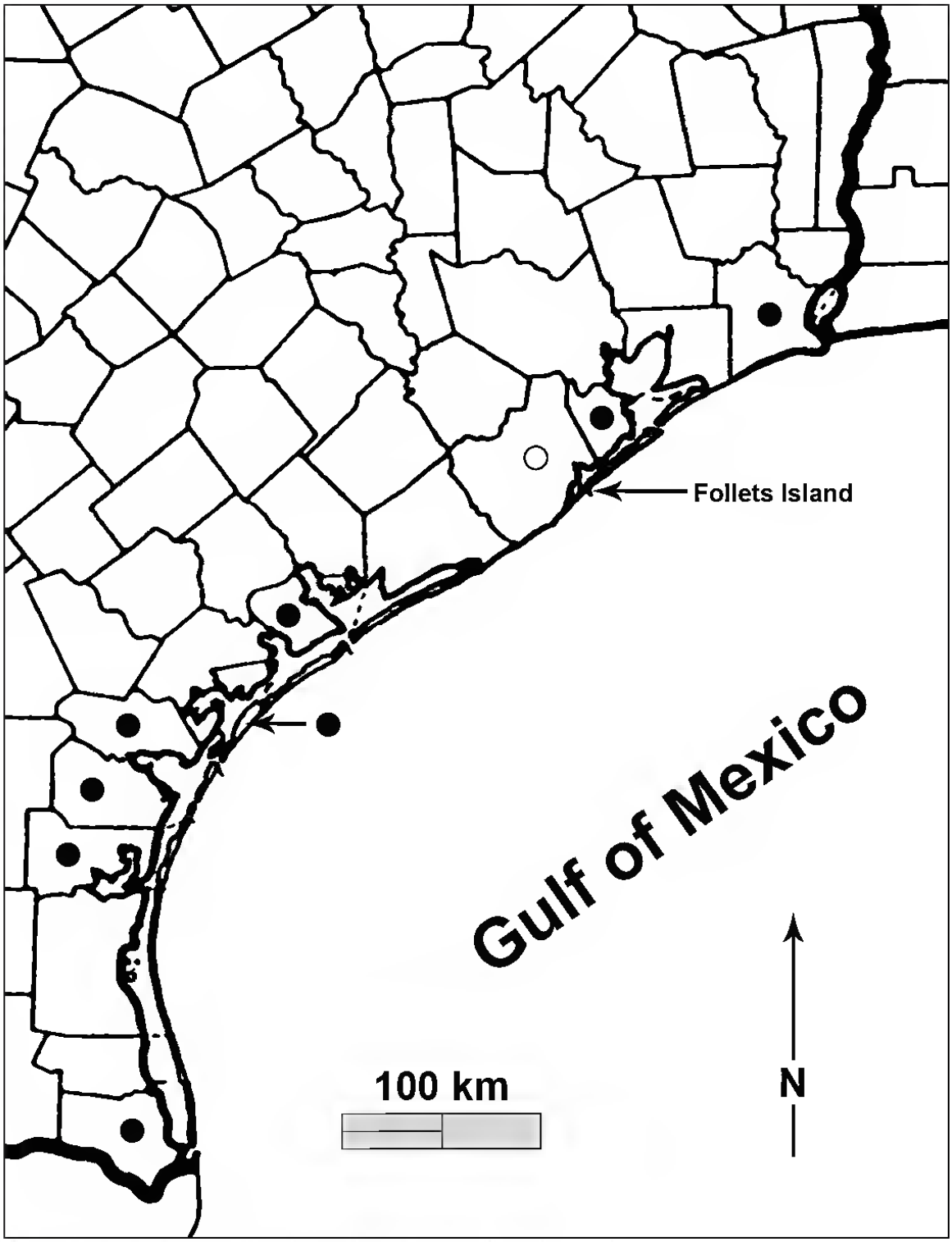

Figure 1 Distribution of *Avicennia germinans* in Texas, including previously reported (•) and a new record from Brazoria County (○).

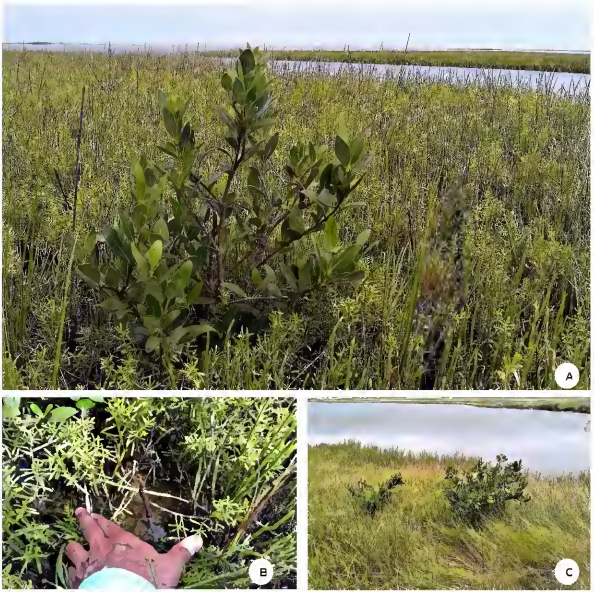

Figure 2. *Avicennia germinans* on Follets Island in Brazoria County, Texas.

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SIDA LITTORALIS, A NEW NAME FOR A SPECIES OF *SIDA* SECT. *ELLIPTICIFOLIAE* (MALVACEAE) ENDEMIC TO FLORIDA

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ABSTRACT

Sida littoralis Siedo, **nom. nov.**, is proposed as a new name to replace *S. floridana* Siedo (not *S. floridana* Gand. [syn = *Malvastrum corchorifolium* (Desr.) Britt. ex Small]) for a species endemic to the state of Florida, USA. A key to the species of *Sida* sect. *Ellipticifoliae* is included to facilitate identification.

RESUMEN

Sida littoralis Siedo, **nom. nov.**, se propone como un nuevo nombre para reemplazar *S. floridana* Siedo (non *S. floridana* Gand. [syn = *Malvastrum corchorifolium* (Desr.) Britt. ex Small]) para una especie endémica del estado de Florida, EE.UU. Una clave para las especies del *Sida* sect. *Ellipticifoliae* se incluye para facilitar identificación.

While reviewing the current literature concerning the genus *Sida* L., a hitherto unknown publication by M. Gandoger (1924) came to the author's attention. Several new species of *Sida* were described in this short paper, including *S. floridana* Gand. Examination of the type material for this name, *S.M. Tracy 6639*, revealed that this specimen is conspecific with *Malvastrum corchorifolium* (Desr.) Britt. ex Small and that *S. floridana* Gand. does not correspond to material of the taxon named *S. floridana* Siedo. The name *S. floridana* Gand. was virtually unknown to the botanical community at the time *S. floridana* Siedo was published in 2001, in spite of the consultation of numerous literature and nomenclature references, including Fryxell (1979, 1985, 1988, 1989), IPNI (2000), Adams (1972), Long and Lakela (1971), Britton (1918), Britton and Millspaugh (1920), Clement (1953), Correll and Correll (1982), Cronquist (1980), Small (1933), Fawcett and Rendle (1926), Gooding et al. (1965), Liogier (1981), Questel (1941, 1951), and Urban (1910, 1920). The earlier date of publication of *S. floridana* Gand. renders *S. floridana* Siedo an illegitimate homonym, necessitating a new name for the taxon represented.

SIDA LITTORALIS Siedo, **nom. nov.** Replacing *Sida floridana* Siedo, nom. illeg., Lundellia 4: 69. 2001, not *S. floridana* Gand., Bull. Soc. Bot. France 71: 633. 1924 [syn = *Malvastrum corchorifolium* (Desr.) Britt. ex Small]. **TYPE: USA. Florida.** Lee Co.: Middle Captiva Island, dry soil in waste places, 29 Apr 1967, *W.C. Brumbach 5819* (holotype: GH!; isotype: US!).

Erect, sparingly branched, perennial **herbs** 1–2 m tall. **Stems** greenish to brownish, sparsely and minutely stellate-pubescent to glabrescent. **Laminae** 5–9 cm long, 1–1.8 cm wide, 4–7 times long as wide, linear-elliptic to narrowly elliptic, sometimes weakly rhombiform, basally cuneate, apically acute; margins crenulate-serrate with teeth becoming more dense and pronounced toward apex; lower surface sparsely stellate-pubescent with primary and secondary venation prominently greenish yellow; upper surface glabrescent with sparse, minute, stellate hairs and inconspicuous venation. **Petioles** 4–7 mm long, sparsely stellate pubescent but relatively more so than the adjacent stem. **Stipules** 4–9 mm long, approximately equaling or slightly exceeding the petiole, filiform to linear in shape and often curved or twisted, margins ciliate. **Flowers** axillary, solitary to somewhat congested apically with up to 5 flowers clustered very near the apex of the branch. **Peduncle** 0.5–

0.75 mm long, unarticulated. **Calyx** 7–9 mm long, accrescent in fruit, longitudinally 10-costate with costae corresponding to each lobe and sinus, lobes essentially trullate with acuminate to minutely caudate apices often twisted in dextrorse or sinistrorse fashion; tricolorous, yellowish to greenish cream colored at base, green medially, and dark green at apical margin. **Corolla** 3–3.5 cm in diameter and pale yellow in color. **Staminal column** ca. 4 mm long with simple to branched translucent hairs along the column and lower portion of the filaments. **Gynoecium** of 9–12 filamentiferous styles emerging from the apex of the staminal column. **Schizocarps** 6–7 mm in diameter, apical portion emergent from calyx and purplish-black, basal portion enclosed and cream to slightly greenish, entire fruit blackening with age, apically pubescent with simple or forked antrorse hairs. **Mericarps** 9–12, two-awned at apex, strongly reticulated dorso-laterally on lower hemisphere; prominent purplish-black coloration on exposed apical surfaces, cream colored laterally, and cream to slightly greenish dorso-basally; apically pubescent. **Seeds** smooth, dark brown, puberulent apically and ventro-apically, though in poor condition on the specimens examined.

Additional specimen examined. **USA. Florida.** Lee Co.: Cayo Costa Island, cabbage palm-live oak forest along central E-W path, 8 Apr 1991, *S. Young & S. Herwitz 539* (USF).

As previously discussed (Siedo 2001), *Sida littoralis* is superficially similar to *Sida elliottii* Torr. & A. Gray and is distinguished by its crenulate-serrate leaves and tricolored calyx with acuminate to weakly caudate lobes terminating in a somewhat elongated apical tail often twisted in a dextrorse or sinistrorse fashion. This taxon also has a unique glabrous appearance, though it is evenly pubescent throughout. This is due to the somewhat sparse and minute nature of the fine, stellate-pubescent vestiture with hairs less than 0.1 mm long. This species has weakly rhombic leaf blades which are somewhat similar to the rhombo-elliptic laminae of *S. rubromarginata* Nash, though not as pronounced and without purplish to reddish margins. The latter is readily distinguished from *S. littoralis* by its articulated peduncle, laminae with serrate leaf margins which are purplish to reddish in color, and broadly three-nerved stipules approximately twice the length of the adjacent petiole. *Sida littoralis* flowers in April and is known exclusively from two collections on coastal islands in the Gulf of Mexico in Lee County, Florida.

Artificial Key to the Species of *Sida* Sect. *Ellipticifoliae*

1. Peduncles 6–20 cm long, 1.5–4 times as long as subtending leaves; seeds glabrous.

    2. Laminae linear to lance-linear; plant vestiture of short, stellate hairs less than 0.2 mm long; mericarps bluntly beaked apically, moderately to prominently reticulated dorso-laterally on lower hemisphere; western Texas and northern Coahuila ..... **Sida longipes** A. Gray
    2. Laminae broadly to narrowly elliptic; plants evenly pubescent with stellate-velutinous hairs ca. 0.5 mm long; mericarps blunt apically and weakly reticulated dorso-laterally on lower hemisphere; southern Tamaulipas and central San Luis Potosí ..... **Sida potosina** Brandegee

1. Peduncles 0.5–6 cm long, shorter than or only slightly exceeding subtending leaves; seeds glabrous to apically pubescent.

    3. Laminae 1–4.5 cm long, narrowly to broadly oblong or elliptic, 1.5–6 times long as wide, apically obtuse, rounded or weakly acute; mericarps blunt, rounded to two-awned apically and weakly, if at all, reticulated dorso-laterally on basal hemisphere; peduncles up to 2 cm long, not articulated.

        4. Laminae narrowly elliptic, 2–6 times long as wide, margins serrate; upper surface stellate-pubescent with simple hairs sometimes present; mericarps apically blunt to very weakly spinose, smooth to weakly reticulated dorso-laterally on lower hemisphere, awns up to 0.3 mm long; seeds glabrous to sparsely pubescent apically ..... **Sida linearis** Cav.

4. Laminae elliptic to ovate, 1.5–3 times long as wide, margins dentate; upper surface glabrous to sparsely pubescent with simple hairs; mericarps apically spinose, lower hemisphere smooth, awns up to 1 mm long; seeds prominently pubescent apically with simple or forked hairs ..... **Sida turneroides** Standl.

3. Laminae 2–9 cm long, linear or lance-linear to narrowly elliptic or rhombo-elliptic, 4—21 times long as wide, but if 4–7 times long as wide, leaves acuminate at apex and plants from Florida; mericarps weakly to prominently two-awned apically and dorso-laterally reticulated on lower hemisphere; peduncles 0.5–6 cm long, articulated or not.

5. Stipules 1.5–2 times the length of adjacent petiole, linear; laminae narrowly rhombo-elliptic, 4–6 times as long as wide, glabrate above; seeds pubescent apically and ventro-apically; peduncles 0.5–2(–3) cm long, 0.5–0.75 times the length of the subtending leaf, articulated ca. 0.5–1 cm below the calyx; endemic to peninsular Florida ..... **Sida rubromarginata** Nash

5. Stipules 0.5 times to approximately equal the length of the adjacent petiole, falcate or subulate, not linear; laminae linear, lance-linear to narrowly elliptic, 4–21 times as long as wide, but if 4–6 times as long as wide then leaves crenulate-serrate and peduncle not articulated; seeds glabrous to apically pubescent, usually ventro-apically glabrous; peduncle 0.5–1.25 times the length of the subtending leaf but if articulated then 0.75–1.25 times the length of the subtending leaf; native to the USA, México, and Guatemala.

6. Peduncles 2–6 cm long, approximately equal or somewhat exceeding the subtending leaf, articulated 1–2 cm below the calyx with the articulation becoming most prominent on mature, fruiting peduncles; flowers strictly axillary; native to Texas and western Louisiana ..... **Sida lindheimeri** Engelm. & A. Gray

6. Peduncles 0.5–4.5 cm long, shorter than the subtending leaf (rarely exceeding it in *S. elliottii*), not articulated; flowers axillary to aggregated apically; native to the southeastern USA and México.

7. Laminae margins crenulate-serrate, more densely so toward apex; lower surface venation prominently greenish yellow with venation inconspicuous on upper surface; plants sparsely, minutely stellate-pubescent to glabrescent, appearing glabrous; calyx lobes apically acuminate to weakly caudate, tricolorous, yellowish to greenish cream at base, becoming green and then darker green distally ..... **Sida littoralis** Siedo

7. Laminae margins evenly serrate, venation not conspicuous; plants stellate pubescent on all surfaces, with the possible exception of upper leaf surfaces in *S. elliottii*, which are usually glabrate; calyx lobes apically acute to weakly acuminate; essentially monochrome, green at base.

8. Plants decumbent to ascending, up to 0.5 m tall, diffusely branched basally and lacking a well defined central axis; flowers drying rose colored, usually aggregated apically; calyx stellate pubescent with simple to forked villous hairs along the costae; peduncles to 2 cm long; laminae stellate pubescent above ..... **Sida neomexicana** A. Gray

8. Plants erect, up to 1 m tall, few stemmed with a well defined central axis, not diffusely branched at base; flowers drying yellow, usually axillary (sometimes aggregated apically in southeastern USA populations); calyx with villous hairs present (southeastern USA and southern México to Guatemala) or absent (central to northern México and southern Florida); peduncles 0.5–4 cm long; laminae usually glabrate, sometimes stellate pubescent above (southeastern USA excluding southern Florida) ..... **Sida elliottii** Torr. & A. Gray

9. Calyx stellate-pubescent, usually villous hirsute at base and along costae; flowers axillary to apically congested; laminae linear to narrowly elliptic, purplish along margins or not, glabrate to stellate and simple pubescent above; plants to 1 m tall; southeastern USA excluding southern Florida ..... **Sida elliottii** var. **elliottii**

9. Calyx stellate-pubescent, villous hairs absent; flowers axillary; laminae linear, usually purplish along margins, glabrate above; plants to 0.5 m tall; southern Florida and México ..... **Sida elliottii** var. **parviflora** Chapm.

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ABSTRACT

Thirty-eight plant taxa are reported for Sonora, Mexico, for the first time. Specimens, observations, and images are deposited in herbaria and are available in the SEINet and MABA online databases.

In 2010, Molina-Freaner and Van Devender published *Diversidad Biológica de Sonora*, which summarized the state of knowledge of all major plant and animal groups in Sonora, Mexico. In the chapter on vascular plants, Van Devender et al. (2010) included a list of the flora of the state of Sonora as an appendix. Since then Van Devender and Reina-G. have maintained and updated the state flora list. The Southwest Environmental Information Network (SEINet 2014) is the primary source of herbarium collections from the southwestern USA and northwestern Mexico. Coverage in Mexico is not as comprehensive because the first SEINet efforts were focused on Arizona collections. Data reported here help to fill this information gap.

The Madrean Archipelago Biodiversity Assessment (MABA) program at Sky Island Alliance was started in 2009. This program documents the distributions of all species of plants and animals in the Sky Island Region, especially in Sonora, Mexico. Information comes from historical sources (herbaria, museums, publications, field notes, etc.) and new field collections, observations, and images). Van Devender and Reina-G. were the principal botanists on MABA Expeditions (Sierras Aconchi, Bacadéhuachi, la Huérfana [=Mazatán], la Madera, San Antonio, San Luis, la Púrica, and el Tigre) to document plants and animals in eight isolated Sky Island mountain ranges and numerous smaller inventories of other areas in Sonora. Flesch and Jacobs observed plants as part of breeding

bird inventories in 26 Sky Island mountain ranges and the northernmost Sierra Madre Occidental (Flesch 2014). All of these biological observations and related images are publically available in the MABA database (www.madrean.org). The FLORA part of the database is directly linked to SEINet.

Here we report 38 new plant taxa for the flora of Sonora. Additional significances are added to individual accounts. Specimens identified by specialists are acknowledged; others were determined by the collectors. Most of these range extensions are documented by herbarium specimens, but others are observations and/or photovouchers in the MABA database or SEINet General Observation. Non-native species are indicated with an "*".

SPECIES RECORDS

Amaranthus torreyi (A. Gray) A. Gray ex S. Wats. (Amaranthaceae). MEXICO. **Sonora.** Mpio. de Cucurpe: Palm Canyon, 25 km SE of Magdalena on road to Cucurpe, Sierra Cinta de Plata (= Sierra Babisal), 30°28'13" N, 110°48'31" W, 1049 m, 4 Sep 1976, *Van Devender,* and *Miksacek* (ARIZ; det. J.B. Urry [Bowers]). Mpio. de Agua Prieta: Arroyo Gallardo, 8 km E of Agua Prieta on MEX 2, 31°18'56" N, 109°23'11" W, 1320 m, rare annual on rocky slope in Chihuahuan desert scrub, 10 Sep 2002, *Van Devender 2002-626, Reina-G., Doan, Damrel, Liu,* and *Marussich* (ARIZ).

Cymopterus multinervatus (J.M. Coult. & Rose) Tidestrom (Apiaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Animas Valley, 58.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°19'13" N, 108°54'12" W, 1600 m, uncommon perennial herb in plains grassland, 15 May 2010, *Van Devender 2010-412, Reina-G.,* and *Roll* (ARIZ, USON).

Asclepias quinquedentata A. Gray (Asclepiadaceae). MEXICO. **Sonora.** Mpio. de Moctezuma: Rancho San Fernando, 17.7 km (by air) W of Huásabas, 20.6 km (by air) NE of Moctezuma, E side of the Sierra de la Madera, 29°55'43" N, 109°28'54" W, 1490 m, rare perennial herb; flowers reddish, drying purplish, succulent fasciculate roots in oak woodland, 5 Aug 2010, *Reina-G. 2010-817, Van Devender, Roll, Hedgcock, Yanes-A.,* and *Jacobs* (ARIZ, USON; det. M. E. Fishbein).

Asclepias uncialis Greene (Asclepiadaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Animas Valley, 2.6 km south of MEX 2 (at ca. 62 km east of Agua Prieta), Cuenca Los Ojos Conservation Area, 31.3025° N -108.890278° W, 1616 m, plains grassland, rare perennial herb; flowers purple, 26 Apr 2009, *Reina-G. 2009-64, Van Devender, Anderson,* and *Wilder* (ARIZ).

Significance. First records for Sonora and Mexico.

Artemisia dracunculus L. var. **glauca** (Pall.) Bess. (Asteraceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Rancho el Pinito, Arroyo Cajón Bonito, 56.5 km (by air) ESE of Agua Prieta, Cuenca Los Ojos Foundation Conservation Area, Sierra San Luis, 31°11'26" N, 108°56'27" W, 1432 m, very common herbaceous perennial in shady canyon bottom in sycamore-Arizona cypress-oak canyon forest, 23 Sep 2009, *Van Devender 2009-1469, Reina-G., Roll,* and *Rose* (ARIZ, TEX); 58 km (by air) ESE of Agua Prieta, 31°12'00" N, 108°56'24" W, 1427 m, abundant herbaceous annual/perennial in disturbed grazed area in riparian vegetation, 25 Sep 2009, *Reina-G. 2009-1556,* and *Van Devender* (ARIZ, MEXU, TEX, USON); above Arroyo Cajón del Diablo, northwestern Sierra San Luis, 2.7 km S of MEX 2 (at 80 km E of Agua Prieta), ca. 66.9 km (by air) E of Agua Prieta, Cuenca Los Ojos Conservation Area, 31°17'33" N, 108°41'56" W, 1766 m, locally common herbaceous perennial, flowers whitish-yellow in *Arctostaphylos-Quercus-Juniperus* chaparral, 29 Sep 2009, *Van Devender 2009-1729 & 2009-1733, Reina-G., Schmidt,* and *Turner* (TEX, USON; ARIZ, TEX). All det. B.L. Turner.

Brickellia veronicifolia (Kunth) A. Gray (Asteraceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Rancho el Pinito, Arroyo Cajón Bonito, 56.5 km (by air) ESE of Agua Prieta, Cuenca Los Ojos Foundation Conservation Area, Sierra San Luis, 31°11'26" N, 108°56'27" W, 1432 m, uncommon subshrub in sycamore-Arizona cypress-oak canyon forest, 23 Sep 2009, *Van Devender 2009-1426, Reina-G., Roll,* and *Rose* (ARIZ, TEX; det. B.L. Turner, 2011).

Cirsium undulatum (Nutt.) Spreng. (Asteraceae). MEXICO. **Sonora.** Mpio. de Cananea: vicinity of Observatorio Astrofisico "Guillermo Haro", Sierra la Mariquita, 9.4 km (by air) NNW of Cananea, 31°03'16" N, 110°22'57" W, 2422 m, common on hill top in pine-oak forest with *Pinus strobiformis,* flowers lavender, 19 Sep 2010, *Reina-G. 2010-928, Van Devender, Sánchez-E., Roll,* and *Sartain* (TEX, USON; det. B.L. Turner, 2011). Mpio. de Ímuris: Rancho el Salto, 27.4 km (by air) ESE of Ímuris, Sierra Azul, 30°44'27" N, 110°34'21" W, 2458 m, uncommon herb, flowers purple-lavender in pine forest, antenna area, 4 Oct 2010, *Van Devender 2010-1036, Reina-G., Sánchez-E.,* and *Delgado* (TEX; det. B.L. Turner, 2011).

***Cotula australis** (Spreng.) Hook. f. (Asteraceae). MEXICO. **Sonora.** Mpio. de Ímuris: Rancho Agua Caliente, 17.2 km (by air) N of Ímuris, 30°57'13" N, 110°51'11" W, 975 m, common ground cover with yellow flowers in cottonwood-willow gallery forest, 28 Mar 2010, *Reina-G. 2010-343,* and *Van Devender* (ARIZ, MEXU, TEX, USON; det. B.L. Turner, 2011).

Significance. Native to Australia and New Zealand.

Helianthus arizonensis R.C. Jackson (Asteraceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Rancho la Bota, Animas Valley, ca. 57.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Conservation Area, 31°19'19" N, 108°54'18" W, 1590 m, locally abundant herbaceous perennial on disturbed roadside in Plains grassland, 29 Sep 2009, *Van Devender 2009-1740, Reina-G., Schmidt,* and *Turner* (ARIZ, MEXU, TEX, USON; det. B.L. Turner).

Hymenopappus lugens Greene (Asteraceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Ánimas Valley, 60.1 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'05" N - 108°52'51" W, 1596 m, locally common perennial herb with yellow disk flowers in *Nolina* plains grassland, 17 May 2010, *Van Devender 2010-505, Reina-G.,* and *Roll* (ARIZ, MEXU, NMC, TEX, USON).

Pyrropappus pauciflorus (D. Don) DC. (Asteraceae). MEXICO. **Sonora.** Mpio. de Cucurpe: Ciénega de Saracachi, Rancho Agua Fría, Río Saracachi, 10.6 km (by air) ENE of Cucurpe, rare herbaceous perennial in grassy area with flowers light yellow in cotton-willow riparian forest and mesquite bosque and desert grassland on slopes, 30°21'35" N -110°35'53" W, 946 m, 6 Oct 2010, *Van Devender 2010-1127, Reina-G., Luna,* and *Reyes* (TEX; det. B.L. Turner).

Ratibida columnifera (Nutt.) Woot. & Standl. (Asteraceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Rancho los Ojos Calientes, ca. 49.0 km (by air) ESE of Agua Prieta, Cuenca Los Ojos Foundation property, 31.27833° N -109.00111° W, 1294 m, cottonwood-willow riparian forest, 28 Sep 2009, *Reina-G. 2009-1655, Van Devender,* and *Schmidt* (TEX, USON).

Rorippa curvisiliqua (Hook.) Bessey ex Britt. (Brassicaceae). MEXICO. **Sonora.** Mpio. de Hermosillo: Old Río Sonora channel, SW side of Hermosillo, 29°03'43" N -111°01'20" W, 190 m, locally common annual in moist soil above water in gravel quarry, 11 Feb 2014, *Reina-G. 2014-24, Van Devender* (ARIZ, DES, MEXU, NMC, MO, USON; det. A. Salywon).

Thelypodium wrightii A. Gray var. **wrightii** (Brassicaceae). **Mexico. Sonora.** Mpio. de Agua Prieta: Ojo Caliente Ciénega, Rancho los Ojos, ca. 50 km (by air) ENE of Agua Prieta, Cuenca Los Ojos Foundation Conservation Area, 31.2833° N -108.989722° W, 1410 meters, large wet ciénega with desert grassland/oak slopes above, uncommon 1.5 m tall perennial herb, flowers whitish, 28 Sep 2009, *Reina-G. 2009-1645, Van Devender,* and *Bourns* (ARIZ., DES); Rancho El Diablo, Arroyo Cajón Bonito, Cuenca Los Ojos Foundation property, 45.6 km (by air) ESE of Agua Prieta, 31.290833° N -109.044722° W, 1252 m, cottonwood gallery forest, small herb on rock ledge, flowers white, 16 May 2010, *Reina-G. 2010-472, Van Devender,* and *Roll* (DES); Rancho El Pinito, Arroyo Cajón Bonito, 56.5 km (by air) ESE of Agua Prieta, Cuenca Los Ojos Foundation conservation area, Sierra San Luis, 31.19056° N -108.94083° W, 1432 m, sycamore-Arizona cypress-oak canyon forest, locally uncommon 1.8 m tall herbaceous perennial, flowers white, 23 Sep 2009, *Van Devender 2009-1478, Reina-G., Roll,* and *Rose* (ARIZ., DES, MEXU, TEX, USON); Rancho El Diablo, Arroyo Cajón Bonito, ca. 45.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Conservation Area, 31.29083° N -109.04472° W, 1250 m, cottonwood-sycamore-willow riparian forest, locally common 2.5 m tall herbaceous perennial; flowers white, 1 Oct 2009, *Van Devender 2009-1801, Reina-G., Schmidt, Turner,* and *Trinks* (ARIZ, DES, MEXU, TEX, USON); Rancho El Pinito, Cajón Bonito, Sierra San Luis, Cuenca Los Ojos Foundation, 56.5 km (by air) ESE Agua Prieta, 31.19056° N -108.94083° W, 1432 m, rocky stream canyon, riparian forest with *Platanus wrightii* and *Quercus* ssp., desert grassland on slopes, 7 Sep 2009, *Reina-G. 2009-1518, Van Devender, Roll,* and *Rose* (MABA observation). All det. A. Salywon.

Chenopodium rubrum L. (Chenopodiaceae). **Mexico. Sonora.** Mpio. de Agua Prieta: E of Rancho La Bota, Ánimas Valley, 57.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'44" N, 108°53'52" W, 1609 m, common prostrate, reddish, rosette annuals in disturbed soil on flats in plains grassland, 17 May 2010, *Van Devender 2010-500, Reina-G.,* and *Roll* (ARIZ, CAS, MEXU, USON).

Significance. First records for Sonora and Mexico.

Croton lindheimerianus Scheele (Euphorbiaceae). **Mexico. Sonora.** Mpio. de Moctezuma: 19.6 km SSE of Moctezuma on road to Tepache (SON 117), 29°38'52" N, 109°35'09" W, 672 m, occasional erect annual in heavily grazed area (abundant in nearby area) on basalt cobble plain with dwarf foothills thornscrub, 19 Oct 2003, *Van Devender 2003-1232, A.L. Reina-G.* (ARIZ, IEB, MEXU, MICH, NMC, TEX, USON; det. P.E. Berry, 2006); 20.5 km SSE of junction with Moctezuma-Huásabas Hwy on road to Tepache (SON 117), 29°38'36" N, 109°34'32" W, 689 m, solitary small annual plant in basalt cobble plain with sparse open foothills thornscrub, solitary small annual plant in basalt cobble plain with sparse open foothills thornscrub, 26 Apr 2004, *Van Devender 2004-402, Reina-G., Doan, Ferguson, Liu, Anderson,* and *Johnson* (IEB); 28.1 km SSE of Moctezuma on road to Tepache (SON 117), 29°38'19" N, 109°33'52" W, 696 m, solitary large annual at edge of pavement in basalt cobble plain with dwarf foothills thornscrub, 14 Aug 2006, *Reina-G. 2006-540,* and *Van Devender* (ARIZ, CAS, HCIB, IEB, MICH, MEXU, MO, TEX, US, USON).

Significance. First records for Sonora and Mexico. Disjunct population of a Chihuahuan Desert species.

Dalea enneandra Nutt. (Fabaceae). **Mexico. Sonora.** Mpio. de Sahuaripa: 25.3 km (by air) NNE of Sahuaripa, 29°15'45" N, 109°07'53" W, 774 m, locally common erect herb, flowers blue, 1 Sep 2009, *Van Devender 2009-613, Reina-G., Minter, Hinojo-Hinojo, Delgado-Z.,* and *Gómez* (ARIZ, CAS, HCIB, MEXU, MO, NMC, TEX, US, USON; det. M. McMahon, 2010); 36 km (by air) NNE of Sahuaripa, Reserva del Jaguar del Norte, 29°23'32" N, 109°08'01" W, 800 m, uncommon erect herbaceous perennial, flowers blue, 1 Sep 2009, *Van Devender 2009-708, Reina-G., Minter, Hinojo-Hinojo, Delgado-Zamora, Gómez-R.,* and *Ramírez* (ARIZ, MEXU, USON). All det. S. McMahon.

Significance. Disjunct population of a Chihuahuan Desert species.

Desmanthus pumilus (Schltdl.) J.F. Macbr. var. *pumilus* (Fabaceae). MEXICO. **Sonora.** Mpio. de Bacadéhuachi: SE edge of Bacadéhuachi, 29°47'49" N, 109°08'11" W, 692 m, rare prostrate herbaceous perennial with white flowers on disturbed roadside in riparian area in foothills thornscrub, 23 Jul 2008, *Van Devender 2008-305, Reina-G.,* and *Loyola-R.* (ARIZ, MEXU, MO, NMC, TEX, USON; det. A. Delgado-Salinas). Mpio. de Cananea: 10 km al S de Cananea, carretera a Arizpe, Lat. 30 56' N; 110 16' W, 1340 m, hierba postrada de flores blancas, abundante en pastizal, suelo inundable, 20 May 1987, P. Tenorio-L. 13573 (MEXU).

Lupinus argenteus Pursh (Fabaceae). MEXICO. **Sonora.** Mpio. de Bacadéhuachi: Sierra Bacadéhuachi, upper Arroyo El Chorro, 1.8-2.5 km (air) NNE Cerro La Placa, on ridgetop locally called Pico de La Cruz (at 11.5 km E and 6 km N Bacadéhuachi), "espuela" fide A. Valencia-Cordova, 29.85833° N -109.025° W, 2300 m, rocky rhyolite soil, N, W, and SW slopes, 10 Dec 1995, *Ferguson 834, M. Kaib, Mata-Mangueros,* and *Valencia-Cordova* (ARIZ; det. M. Fishbein)

***Prosopis glandulosa** Torr. var. **glandulosa** (Fabaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: W base of Sierra San Luis, canyon south of MEX 2, 70.6 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°19'17" N, 108°46'43" W, 1750 m, solitary 2.0 m tall shrub on roadside in oak woodland, 17 May 2010, *Van Devender 2010-488, Reina-G.,* and *Roll* (ARIZ, ASU, HCIB, MEXU, MO, NMC, TEX, US, USON).

Significance. A Texas variety likely spread from cattle trucks along MEX 2.

Sophora nuttalliana B.L. Turner (Fabaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Ánimas Valley, 68.9 km E of Agua Prieta on MEX 2, Cuenca Los Ojos Conservation Area, 31°19'26" N, 108°56'03" W, 1599 m, herbaceous perennial in dense patch growing through asphalt on edge of highway in plains grassland, flowers whitish, calyx bluish, 1 May 2008, *Van Devender 2008-83,* and *Reina-G.* (ARIZ, ASU, HCIB, MEXU, MO, NMC, OJOS, TEX, USON; det. R. Spellenberg); just south of New Mexico border, W side Ánimas Valley, 54.2 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°19'49" N, 108°57'25" W, 1613 m, locally common perennial herb under 'Normandy barriers' on border and in nearby drainage in plains grassland, flowers white with bluish cast to buds, 19 May 2010, *Van Devender 2010-565,* and *Reina-G.* (ARIZ, TEX, USON). Mpio. de Naco: 13.3 km (by air) SSE of Naco, along MEX 2, 31.210278° N -109.8925° W, 1520 m, single large patch on roadside; flowers white with bluish tint to buds in desert grassland, 21 May 2010, *Van Devender 2010-607,* and *Reina-G.* (ARIZ, CAS, HCIB, MEXU, MO, TEX, USON).

Quercus sideroxyla Bonpl. (Fagaceae). MEXICO. **Sonora.** Mpio. de Nácori Chico, Pico de la India, 4.6 km (by air) S of Mesa Tres Ríos, 29.80234° N -108.70709° W, 2302 m, pine-oak forest, 18 Jun 2012, *Flesch, Valenzuela-A.,* and *González-S.*; Pico de la India, 12.4 km (by air) SSE of Mesa Tres Ríos, 29.73523° N -108.68379° W, 2363 m, pine-oak forest, 19 Jun 2012 *Flesch, Valenzuela-A.,* and *González-S.*; Pico de la India, 11.0 km (by air) S of Mesa Tres Ríos, 29.75126° N 29.75126° W, -108.68777°W, 2224 m, pine-oak forest, 19 Jun 12, *Flesch, Valenzuela-A.,* and *González-S.*; Sierra el Macho, above Pinos Altos, 9.7 km (by air) WSW of Mesa Tres Ríos, 29.78719° N -108.79998° W, 2121 m, pine-oak forest, 30 Jun 2012, SSE of Mesa Tres Ríos, 29.73523° N -108.68379° W, 2363 m, pine-oak forest, 19 Jun 2012, *Flesch, Valenzuela-A.,* and *González-S.* (all MABA observations/ photos; ver. G.M. Ferguson, R. Spellenberg).

Veratrum californicum Durand (Liliaceae). MEXICO. **Sonora.** Mpio. de Huachinera: near Cebadilla on road from Huachinera to Mesa Tres Ríos, 27.3 km (by air) SSE Huachinera, Sierra Huachinera, 29°59'34" N, 108°50'20" W, 1388 m, locally abundant perennial herb in meadow in pine-oak forest, 11 Jun 2005, *D. Danforth* (MABA photo; ver. R.S. Felger, R. Spellenberg).

Hexalectris grandiflora (A. Rich. & Gal.) L.O. Williams (Orchidaceae). **Mexico. Sonora.** Mpio. de Huachinera: 14.4 km (by air) SSE of Huachinera, Sierra Huachinera, 30.08536° N -108.898° W, 2000-2100 m, pine-oak forest, 3 Aug 2006, *Jacobs* and *Flesch* (SEINet General Observation photo, ver. R. A. Coleman).

Hexalectris spicata (Walter) Barnhardt var. **arizonica** (S. Watson) Catling & V.S. Engel (Orchidaceae). **Mexico. Sonora.** Mpio. de Ures: 11.8 km (by air) NNW of Mazatán, Sierra de Mazatán (= Huérfana), 29.1011° N -110.196389° W, 1420 m, oak woodland, in oak duff among boulders under *Quercus* canopy in partial shade, six flower spikes to 48 cm height, robust, leafless, 2 Oct 2005, *Wilson* (photovouchers: ARIZ, ASU, DES, HCIB, MEXU, TEX, USON, UTEP, det. G.A. Salazar-Chávez).

Hexalectris warnockii Ames & Correll (Orchidaceae). **Mexico. Sonora.** Mpio. de Ures: 11.9 km (by air) NNW of Mazatán, Sierra de Mazatán (= Huérfana), 29.10639° N -110.19694° W, 1400 m, oak woodland, in oak duff among boulders on S-facing slope in partial shade, 8 Sep 2008, *Wilson* (photovouchers: ARIZ, ASU, DES, HCIB, MEXU, TEX, USON, UTEP, MABA photos, ver. R. A. Coleman, G.A. Salazar-Chávez).

Malaxis novogaliciana R. González ex McVaugh (Orchidaceae). **Mexico. Sonora.** Mpio. de Bacadéhuachi: Rincón de Guadalupe, 16.5 km (by air) ENE of Bacadéhuachi, Arroyo Campo los Padres (Río Riito drainage), Sierra de Bacadéhuachi, 29.8444° N -108.9769° W, 1680 m, rocky canyon and mountainside, 05 Sep 2011, *Reina-G. 2011-632A, Van Devender, Bygott,* and *Palting* (MEXU, USON; det. G.A. Salazar-Chávez).

Sarcoglottis schaffneri (Rchb. f.) Ames (Orchidaceae). **Mexico. Sonora.** Mpio. de Moctezuma: Rancho San Fernando, 17.7 km (by air) W of Huásabas, 20.6 km (by air) NE of Moctezuma, E side of the Sierra de la Madera (= Oposura), 29.9286° N -109.48167° W, 1490 m, rare perennial herb with basal rosette of leaves and succulent fasciculated roots in oak woodland, 5 Aug 2010, *Reina-G. 2010-774A, Van Devender, Yanes-A., Roll,* and *Jacobs* (MEXU, USON; det G.A. Salazar-Chávez).

Penstemon fendleri Torr. & A. Gray (Plantaginaceae). **Mexico. Sonora.** Mpio. de Agua Prieta: Ánimas Valley, 60.9 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'19" N, 108°53'14" W, 1610 m, rare perennial herb with purple flowers in *Nolina* plains grassland, 15 May 2010, *Van Devender 2010-393, Reina-G., Enderson,* and *Roll* (ARIZ).

Alopecurus carolinianus Walter (Poaceae). **Mexico. Sonora.** Mpio. de Agua Prieta: Ánimas Valley, 60.1 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'27" N, 108°55'28" W, 1644 m, very common annual in dried mud in stock tank in plains grassland, 20 May 2010, *Reina-G. 2010-595,* and *Van Devender* (ARIZ, MEXU, NMC, USON); just S of New Mexico border, W side Ánimas Valley, 54.2 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°19'49" N, 108°57'25" W, 1613 m, locally abundant annual in moist soil in shallow drainage in plains grassland, 19 May 2010, *Van Devender 2010-558,* and *Reina-G.* (ARIZ, CAS, HCIB, MO, TEX, USON, US).

Significance. First records for Sonora and Mexico.

Elymus canadensis L. (Poaceae). **Mexico. Sonora.** Mpio. de Agua Prieta: Rancho El Cajón Bonito, 6.3 km southeast of MEX 2 (at 53 km east of Agua Prieta), Cuenca Los Ojos conservation area, 31.2783° N -109.0011° W, 1291 m, cottonwood willow riparian forest, 16 Aug 2007, *Reina-G. 2007-795,*and *Van Devender* (ARIZ, MEXU, NMC, USON; det. C.G. Reeder); Ciénega Ojo Caliente, Rancho los Ojos, ca. 50 km (by air) ENE of Agua Prieta, Cuenca Los Ojos Foundation conservation

area, 31.2833° N -108.98972° W, 1410 m, large wet ciénega with desert grassland/oak woodland on slopes above, 28 Sep 2009, *Reina-G. 2009-1606, Van Devender,* and *Bourns* (ARIZ, MEXU, USON); Rancho los Ojos, Cajón Bonito, ca. 49.2 km (by air) ESE of Agua Prieta, 6.3 km SE of MEX 2 (at 53 km E of Agua Prieta), Cuenca Los Ojos Foundation Conservation Area, 31.27833° N -109.0011° W, 1291 m, in sand near stream in cottonwood-willow riparian forest, 30 Sep 2009, *Reina-G. 2009-1758, Van Devender, Schmtdt,* and *Turner* (NMC, US, USON); Rancho el Diablo, 45.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31.29083° N -109.04472° W, 1250 m, canyon bottom, rocky slope in cottonwood-sycamore-willow riparian forest, shrubby desert grassland on slopes, 1 Oct 2009, *Van Devender 2009-1807,* and *Reina-G* (ARIZ, ver. M. Bauer).

*__Hordeum vulgare__ L. var. __trifurcatum__ (Schltdl.) Alef. (Poaceae). MEXICO. **Sonora**. Mpio. de Aconchi: Cerro la Huertita, 12.5 km (by air) WSW of Aconchi, Sierra Aconchi, 29°48'18" N, 110°21'12" W, 1860 m, disturbed roadside in open pine-oak forest, 3 Sep 2012, *Van Devender 2012-568, Hanby, Reina-G.,* and *Loyola-R.* (ARIZ, USON, det. M. Bauer).

Stipa neomexicana (Thurb.) Scribn. (Poaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Ánimas Valley, 60.1 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'05" N, 108°52'51" W, 1596 m, occasional perennial in *Nolina* plains grassland, 20 May 2010, *Reina-G. 2010-601,* and *Van Devender* (ARIZ, CAS, HCIB, MEXU, NMC, MO, TEX, USON); just south of New Mexico border, W side Ánimas Valley, 54.2 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°19'48" N, 108°57'25" W, 1613 m, uncommon perennial on grassy hillside in plains grassland, 19 May 2010, *Van Devender 2010-552,* and *Reina-G.* (ARIZ, MEXU, USON).

Urochloa panicoides P. Beauv. (Poaceae). MEXICO. **Sonora.** Mpio. de Nacozari de García: Rancho Viejo (part of Rancho el Salto), Arroyo el Schick, 17.2 km (by air) N of Nacozari, Sierra la Purica. 30°31'50" N, -109°43'19" W, 1657 m, locally very common prostrate perennial, rocky canyon in oak woodland, 8 Sep 2013, *T.R. Van Devender 2013-178, A.L. Reina-G., Vera Markgraf* (ARIZ, MO; det. G. Davidse).

Phlox gracilis (Douglas ex Hook.) Greene (Polemoniaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: E of Rancho La Bota, Ánimas Valley, 57.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'44" N, 108°53'52" W, 1609 m, locally common annual with white flowers in disturbed plains grassland, 17 May 2010, *Van Devender 2010-502, Reina-G.,* and *Roll* (ARIZ, MEXU, RSA, TEX, USON); ca. 0.5 mi W of Mababi Ranch, ca. 42 mi W of Rte 19, along turnoff 3.2 mi N of Esqueda, 30.771304° N -109.892021° W, 1270 m, rocky hillside, along stream, 27 Mar 1970, *McGill 6420, Pinkava* (ASU, det. E. Lehto)

Delphinium wootonii Rydb. (Ranunculaceae). MEXICO. **Sonora.** Mpio. de Agua Prieta: Ánimas Valley, 60.9 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'19" N, 108°53'14' W, 1610 m, rare perennial herb with pale lavender flowers in *Nolina* plains grassland, 15 May 2010, *Van Devender 2010-389, Reina-G., Roll,* and *Enderson* (HCIB, TEX, USON); E of Rancho La Bota, Ánimas Valley, 57.7 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°18'44" N, 108°53'52" W, 1609 m, locally common annual, flower pale lavender in plains grassland, 17 May 2010, *Van Devender 2010-504, Reina-G.,* and *Roll* (MEXU, USON) and solitary individual with albino flowers, 17 May 2010, *Van Devender 2010-504A, Reina-G.,* and *Roll* (ARIZ); Arroyo Guadalupe, Rancho Puerta Blanca, Cuenca Los Ojos, Foundation property, ca. 41 km E of Agua Prieta on MEX 2, 31°18'57" N, 109°05'35" W, 1295 m, locally common in side canyon with pale lavender flowers in desert grassland, 16 May 2010, *Reina-G. 2010-423, Van Devender,* and *Roll* (ARIZ, CAS, MEXU, MO, NMC, USON); just S of New Mexico border, W side Ánimas Valley, 54.2 km (by air) E of Agua Prieta, Cuenca Los Ojos Foundation property, 31°19'49" N,

108°57'25" W, 1613 m, locally uncommon annual with lavender flowers in plains grassland, 19 May 2010, *Van Devender 2010-569,* and *Reina-G.* (ARIZ, US, USON).

Potentilla norvegica L. (Rosaceae). MEXICO. **Sonora.** Mpio. de Sahuaripa: Rancho El Refugio at Río Áros, Arroyo Las Tésotas, 29°25'02" N, 109°05'01" W, 488 m, rare annual in sand next to river, riparian vegetation with foothills thornscrub on slopes, 30 Mar 2011, *Van Devender 2011-48, Reina-G., Duarte-R., Gómez-R., Gutiérrez-G.,* and *Gómez-M.* (ARIZ).

***Ruta graveolens** L. (Rutaceae). MEXICO. **Sonora.** Mpio. de Nacozari de García: church above Mina El Tigre, 33.1 km (by air) WNW of Bavispe, 46.2 km (by air) ENE of Nacozari de García, Sierra el Tigre, 30°35'22" N, 109°13'07" W, 1831 m, occasional 0.5 m tall herb along trail with strong odor to foliage in oak woodland, established cultivar away from house ruins, 17 Mar 2010, *Reina-G. 2010-171, Van Devender, Portillo, Jimenez-M.,* and *M. Munguia* (ARIZ); Pilares de Téras, 35.8 km (by air) NW of Bavispe, 51.1 km (by air) ENE of Nacozari de García, 30°39'01" N, 109°15'29" W, 1101 m, locally common herb below abandoned houses in riparian vegetation with *Populus monticola,* Sonoran desertscrub on slopes, 21 Mar 2010, *Reina-G. 2010-306,* and *Van Devender* (confiscated by APHIS at border).

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A NEW SPECIES OF *CALYPTRANTHES* (MYRTACEAE) FROM PANAMA

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ABSTRACT

A new species of Myrtaceae from Panama, *Calyptranthes straminea* B. Holst, is described and illustrated. It is most closely similar to *C. contrerasii* Lundell from Guatemala, with which it shares cordate to subcordate leaves and and narrowly winged stems.

Thirty-seven species of *Calyptranthes* (Myrtaceae) were recently treated in Flora Mesoamericana (Holst & Kawasaki 2009). While reviewing a collection made in the wet, lowland forest of Colón Province, Panama, at the mining concession Minera Panama SA (previously Teck Cominco Petaquilla), it was immediately clear that one specimen represented a new addition to the Flora and a new species for science.

While most *Calyptranthes* species are distinguished by their bifurcate vegetative branching, paired panicles, and circumscissile flowers, the distinction lessens in certain parts of South America and becomes muddled with its closest relatives, *Myrcia* and *Marlierea*. However, following current generic concepts, the species described here clearly falls into *Calyptranthes*.

CALYPTRANTHES STRAMINEA B. Holst, **sp. nov.** **TYPE: PANAMA. Colón:** Teck Cominco Petaquilla mining concession, near helipad, 190 m, 8° 50' 05" N, 80° 39' 45" W, 21 Jun 2008 (fl), *G. McPherson 20568* (holotype: PMA!; isotypes: F, K, MO!, SEL!). Figures 1,2.

Calyptranthes straminea appears related to *C. contrerasii* Lundell from Guatemala. Both species have cordate to subcordate leaves and narrowly winged stems. The new species differs by having numerous flowers per panicle (40–50 vs. to 5), mostly obovate to elliptic leaf blades (vs. ovate to lanceolate), and abruptly narrowed, shortly acuminate leaf apices (vs. evenly narrowed to an obtuse or acute apex).

Tree, 9 m tall; mostly glabrous, with few sparse trichomes present at base of flowers; bark unknown, youngest branchlets narrowly winged, becoming complanate with age. **Leaves** sessile, the blades drying grayish to greenish brown adaxially, usually with a rusty color along the adaxial midvein especially basally, light brown abaxially, obovate to elliptic, 9.5–11 × 4–5.5 cm, chartaceous when dry, glabrous, midvein narrowly sulcate adaxially, prominently convex abaxially, secondary veins 12–18 pairs, slightly ascending, inconspicuous adaxially, visible though not prominent abaxially, marginal vein 2–2.5(–3.5) mm from the margin and gently arching between the secondary veins, the outer 1 mm of the margin revolute, apex abruptly narrowed to a 6–10 mm long, conduplicate-reflexed acumen, base subcordate, somewhat amplexicaul, glands not visible or only scarcely so adaxially, slightly more visible abaxially with magnification. **Inflorescences** panicles, either paired or reduced to one per axil, borne on leafy branches toward branch apices, 5–6 × 2–4 cm, 40–50-flowered, occasionally subtended by a leafy bract to 1 cm long that appears to be caducous at or before anthesis; peduncles 2–4 cm long, ca. 1.5 mm wide, peduncle and lateral axes stramineous, heavily gland-dotted, relatively broad compared to flower bud width, glabrous. **Flowers** short-pedicellate, the pedicel 0.5 mm long, buds 1.5–2.0 mm long, globose with a blunt apicule; hypanthium mostly glabrous or with a few sparse, short, broad, and indistinct trichomes basally, hypanthium collar prolonged 1 mm beyond the summit of the hypanthium with thick, leathery walls,

calyptra 1.5–2 mm wide, thin; petals absent; stamens ca. 60, filaments 4 mm long, anther thecae reniform, ca. 0.3 mm long; style gradually narrowing to a punctiform stigma; ovary bilocular, ovules 2 per locule. **Fruit** and seeds unknown.

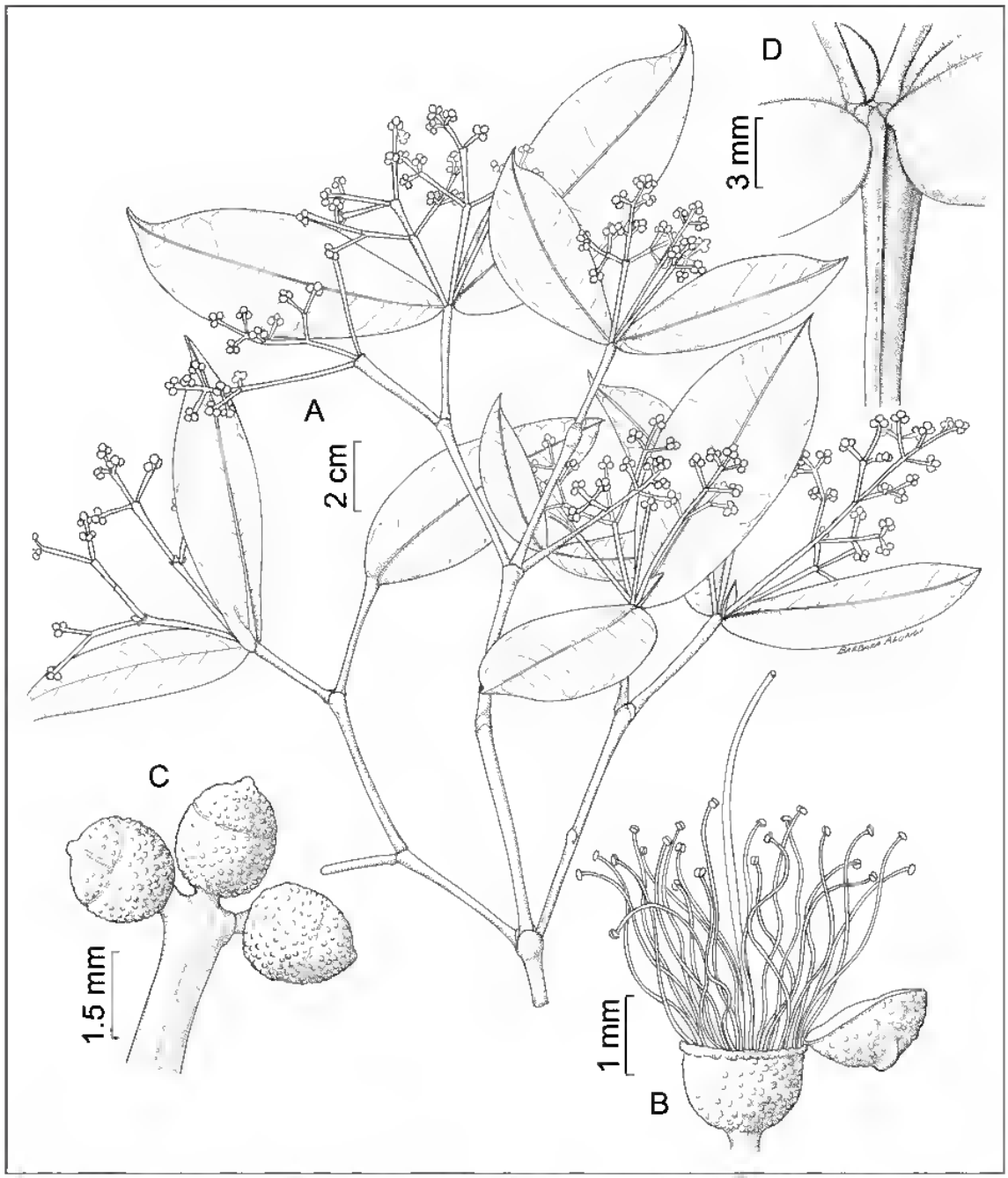

Figure 1. *Calyptranthes straminea* B. Holst. A, habit; B, flower buds; C, detail of flower. Drawn from *G. McPherson 20568* (MO).

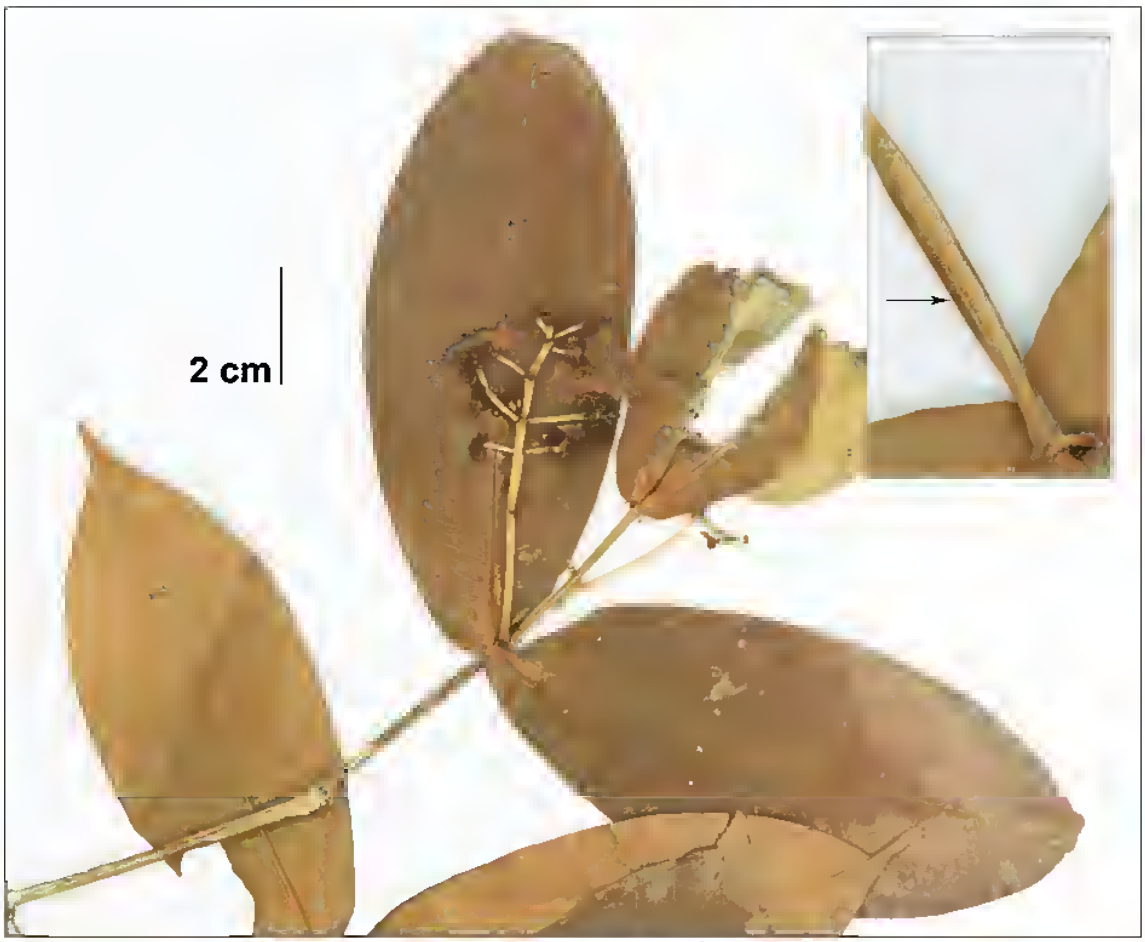

Figure 2 Scan of flowering branch Inset shows narrow branchlet wings From *G McPherson 20568* (SEL)

The collection cited below is completely vegetative and perhaps comes from a branch growing in deep shade Its leaves are larger than the fertile type collection, to 6 × 18 cm

Paratype **PANAMA: Colón:** Coclé del Norte, Area del helipad C10, 108 m, 8° 48' 29" N, 80° 43' 07" W, 28 Aug 2012 (st), *M Laurencio, O Ortiz, & E Sánchez 1032* (MO!, PMA)

Etymology The species epithet *straminea* refers to the straw-colored inflorescence axes when dried, which contrast markedly with the dark brownish flower buds

Conservation Status *Calyptranthes straminea* is known by one fertile and one sterile collection and may be considered data deficient, but it is inherently at risk by being found within a mining concession

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CLASSICAL DETERMINATION OF MONOPHYLY, EXEMPLIFIED WITH *DIDYMODON* S. LAT. (BRYOPHYTA). PART 1 OF 3, SYNOPSIS AND SIMPLIFIED CONCEPTS

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ABSTRACT

Classical systematists introduce evolutionary relationships into classification by identifying monophyly. The classical basis for determining monophyly as serial macroevolution of taxa is here put on a statistical basis. Clues to adaptive or relatively neutral transformative radiation are used in grouping ancestral species and descendant species. Such clues are additive in suggesting a direction of evolution of one taxon to another. These clues are usually intuitive to the informed expert but can be characterized in terms of probabilistic units, decibans. Since decibans are logarithmic they can be added to yield a probability of one species being ancestral to another. Transformative traits are convergent between groups, while conservative traits occur in multiple species and environments in one group. Stem-based evolutionary trees (caulograms) are generated by hypotheses of serial evolutionary change. Although the manner in which evolutionary relationships are evaluated is here considered standard in classical practice, the formalization of scientific heuristic intuition and method of documentation is new. It is hoped that this or a similar method of systematic analysis that creates classifications based on both serial and cladistic evolutionary relationships might be developed and expanded by innovative students and intellectually flexible researchers in systematics.

Given that this paper is mainly intended for motivated classical taxonomists and challengeable students, a synopsis of parts 2 and 3 is given here as a simplified guide to the fundamental concepts and methods. Part 2 gives technical justification and reasons for a new, combined classical-phylogenetic approach. It provides elements of the new method and its statistical basis. Part 3 is a morphologically based example of the method, showing serial evolutionary relationships among species of the moss genus *Didymodon* Hedw. and its close relatives (Pottiaceae, Bryophyta).

Some may feel uncomfortable that the here-recommended use of scientific inductive logic and discursive reasoning results in hypotheses of evolutionary relationships that are not as apparently well-supported as are cladograms in phylogenetics. The choice, however, is between (1) the best attempt at developing theory that addresses all facts including contradictory results in morphological and molecular studies (the method advocated in the present paper), and (2) an exact method that must be wrong much of the time (phylogenetics), as discussed below.

Justification

In morphological cladograms, some descendants from one ancestral species may duplicate traits (as parallelisms) of other descendants, creating false synapomorphies and false branches in a cladogram distal to the ancestral branch. This is probably fairly common given the few traits involved in speciation in any one genus. Or, if one or more descendant species has a reversal in a trait, such species appear lower in the cladogram than the ancestral branch. Examination of traits that are informative of serial transformations (not shared ancestry) can correct false resolution of branch order. A cladistic multifurcation (one ancestor generating multiple descendants) is then entirely appropriate. Evolution of species by serial transformation is here termed transformative radiation.

Parsimony analysis optimizes a cladogram by minimizing the number of trait transformations Naming cladogram nodes further optimizes the cladogram by eliminating unnecessary unknown shared ancestors Thus a "most-parsimonious" cladogram is made even more parsimonious by trimming off nodes that promise resolution that is not really based on shared ancestry (Fig 1) This results in what is in effect a natural key (Zander 2013 82), which can be directly represented by a caulogram Naming cladogram nodes as extant taxa is referred to as "superoptimization"

A cladogram multifurcation remains a poor model of ancestor to multiple descendant relationships because the line below the node is the same taxon as one of the lines coming out of the multifurcation as in Fig 1(2) The best diagram is a caulogram (or commagram, or Besseyan cactus) The polarity of evolutionary diagrams is standard with derived species towards the top, and ancestral species lower Commonly a rooted, stand-alone cladogram or caulogram is understood to be a small area in the apex of a complex tree of life

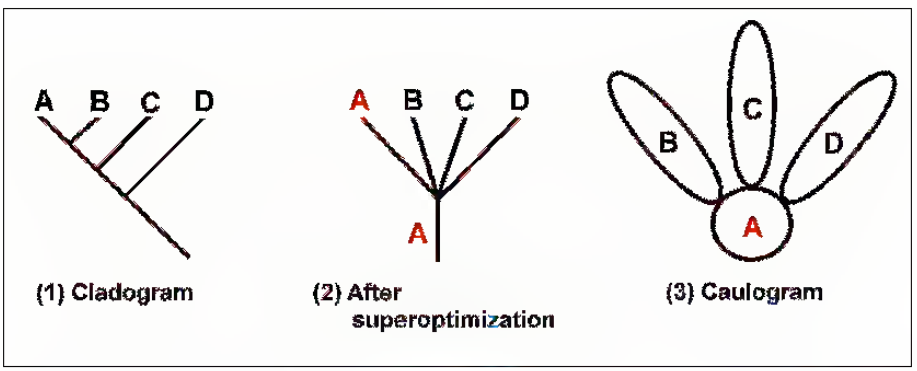

Figure 1 A cladogram (1), here a terminal branch of a larger rooted cladogram, can be changed to a more reasonable multifurcation (2) if A is found to be a taxon ancestral to B, C, and D after analysis for serial transformation The node in the multifurcation (2) is identified as the same taxon as A Because two cladogram branches both representing ancestor A in cladogram (2) are redundant, stem evolutionary relationships are better represented by a caulogram (3) This series simplifies how a cladogram is re-interpreted as a caulogram, wherein a tree of cladistic leaves becomes a tree of evolutionary stems

In molecular studies, cladistic branch order of the molecular strains represented by specimens studied can be estimated to a large extent However, broad-ranging ancestral species may have isolated molecular "strains" even though the molecular strains are essentially identical in expressed traits at the species level

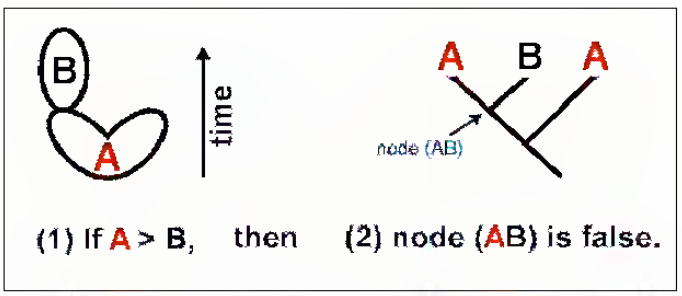

Figure 2 In (1) on left, species A has two extant molecular strains and one of them gives rise to (symbol ">") species B Species A is then ancestral to species B A molecular cladogram (2) distinguishes the molecular strains as separate with B arising from one of the strains If species A is static in expressed traits (i e , the molecular strains genuinely represent the same species), then the node (AB) representing a shared ancestor means little and does not contribute to cladogram resolution of evolutionary relationships between the species

Past speciation events occurring on different strains force the strains apart on a molecular cladogram (Figs. 2-2, 3-1). Strains separated on a cladogram with descendant species in between produce phylogenetic paraphyly. When enough infraspecific strains are sampled, the paraphyly that appears may be interpreted as an ancestral species generating a descendant species. But if one or more molecular strains are extinct or unsampled, uncertainty in branch order is implicit. If paraphyly occurs at, say, one or two nodes distance between strains, then one might expect a similar level of paraphyly among all ancestral species, and given the widespread occurrence of paraphyly in published molecular cladograms, this is a major problem.

Random survival and extinction (or non-sampling) of molecular strains result in random branch order at the level of whatever paraphyly occurs in the group. Evaluation of morphological traits that are not phylogenetically informative can correct the branch order by identifying serial transformation of ancestral and descendant species.

Paraphyly can be simple, with branches for the same taxon only two nodes distant, or it can be more complex, with several nodes between branches leading to samples of the same taxon. Using "shared ancestry" as the sole methodology for phylogenetic reconstruction can result in highly precise but evolutionarily inaccurate (non-monophyletic) cladograms. Evaluation of serial transformations can correct this.

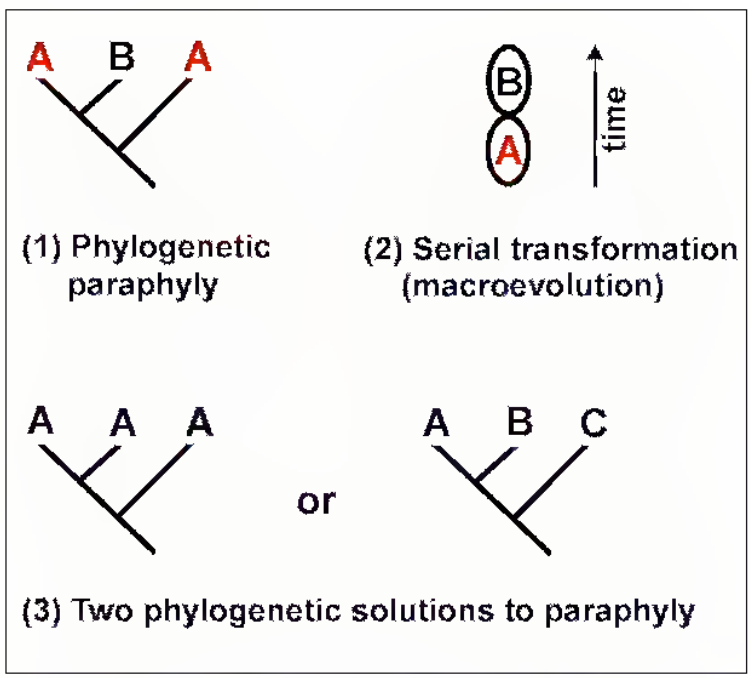

Figure 3. An example of simple phylogenetic paraphyly (1) is one taxon connected to two different nodes on a cladogram. Here species A is represented by two samples, these being distinct molecular strains that appear one node distant from each other (as in Figure 1). Evolutionary systematics suggests that if A is represented by two molecular strains, then B must arise from a deep ancestor of both samples of A. This is a serial transformation that may be represented by a simple caulogram (2). Phylogenetic systematics has two possible solutions (3) that do not abandon the cladogram, either lump the three samples into one taxon as on left, or have one of the A samples represent a new cryptic species as on right. Figure 3 shows problems in both morphological and molecular phylogenetic analysis, in fact at any rank, species through family.

Method

Bayesian statisticians who broke the Nazi war codes during World War II used small clues. The more clues, the better the analysis of the cryptographic code. The basic clue was one **deciban**, or **the minimum probability that will change belief in a hypothesis**. They used Bayesian statistical methods and the methods worked well. For instance, a change from a 0.50 probability (or 50:50 chance of being true) to about 0.55 in favor was considered the minimum clue that a particular hypothesis was true. As explained in detail in Part 3, decibans can be added together to get total probabilities that a hypothesis is true. This is because they are basically logarithmic. One deciban is 0.55 probability, five is 0.75, ten decibans is 0.90, 13 is 0.95, 20 is 0.99.

If you have ten clues of a minimum one deciban each that species A is ancestral to species B, then the chance is 0.90 that you are correct. If the traits examined as clues are very strong evidence of direction of evolution, then two traits at 7 decibans assigned to each will add to 14 decibans and then exceed 0.95 probability. Examples of trait transformations with high deciban values are diploidy → tetraploidy with no evidence of diploidization, widespread relictual habitats → recent habitats, sexual reproduction → asexual reproduction, and generalized morphology → unique specialization. These indications of macroevolutionary transformation between species are well documented in evolutionary texts as examples of (probably unidirectional) taxon transformations.

What you must do first, to make the analysis tractable, is to reduce if possible the species in the group you are studying to smaller groups with only one apparent generalist ancestor plus its apparent derivative species that radiate from it as transformations. These groups can be isolated from a standard dichotomous key to species, where derived species are commonly at the ends of series of couplets. These isolated groups will look like Fig. 1(3), or even Fig. 3(2), or as complex as Fig. 2 in Part 2. Criteria discussed in Part 2 of this paper are helpful. In some cases such groups may be treated as taxonomically distinct (the "dissilient genera" of Zander 2013: 92). Occasionally no generalist ancestor can be found among extant species for certain closely related apparently derived species, in which case a generalist shared ancestral species may be postulated.

For each group studied (in this paper, genera), the probabilities of one species transforming into another are calculated using decibans. Each species is assigned a number of clues that it is derived, based on theory of adaptive or at least rare or unique transformative trait transformations. The clues may be valued variously, but the restriction to 1, 3, 5, or 7 decibans controls guesswork and over-exactitude.

An expert can usually identify one species as apparent ancestor of a small or large cloud of derived species, at least in large genera. If there are more than one central ancestral species, segregation into separate genera (or other supraspecific rank) of each ancestor-species group is justified. A standard dichotomous key or a cladogram may be the first way to cluster species, or a "natural key" (Zander 2013: 47, 82) may be devised. Clues to which species are derived and which are ancestral are discussed in Part 2 of this paper. Assignment of deciban probabilities to various species clarifies direction and serial order of evolution.

For each group comprising one central ancestral species and attendant descendant species, if all species are clearly in that one group, and if one ancestor-descendant transformation is well supported, then all species are descendants of that identified ancestor. This allows one best probability to represent all of the transformation series. The probabilities may not be directly compared (they are not part of one probability distribution), however, because they are each generated by somewhat different data. They are, however, nested, so Bayes factors can be used. In this case Bayes factors are simply calculated as one probability (i.e., likelihood) for a particular hypothesis divided by the probability of another hypothesis. The significance of Bayes factors can be read off a standard table (see Part 2, Table 2).

A critical formula is the Implied Reliable Credible Interval (IRCI) calculation (see Part 2) which calculates the chance that at least one hypothesis has a high chance of being true in cases when you have a lot of hypotheses each with less than acceptable probability of being true. If the IRCI is 0.95 or greater, the question of which is ancestor is decidable. (If one species is demonstrably ancestor of one other species, then it is the ancestor of all of them in the group.) It is decidable is because there is sufficient information that at least one species is ancestor, but you do not know yet which one. A high Bayes factor can then identify which species is ancestor..

Some heuristics of monophyly

Heuristics are rules of thumb that help develop hypotheses or make decisions. Evolution involving modeling serial transformation of one taxon into another is complex and requires judgment, including evaluation of evidence. This paper formalizes (suggests a statistical basis for) analytic heuristics including the following:

1. Taxonomists use clues to evaluate monophyly. Sequential Bayes analysis through deciban assignment adds up clues in the context of a scale of probabilities.

2. Sequential Bayes analysis using decibans is a powerful analytic tool. It is similar to Shannon-Weaver information analysis, which is widely used in decision theory. There is a direct equivalence between decibans and bits, where 1 dB equals about 0.33 bits. The major relevant difference is that one deciban is considered the minimum for a perceived clue, but one bit (3 dB) is the minimum unequivocal unit of information (i.e., that which one may use to make a decision between two alternatives).

3. Identifying radiative transformation is a key element in monophyly estimation. Support for this comes from theory of adaptive radiation; Dollo non-reversal of large sets of traits, particularly those of whole taxa, being considered very rare in nature; and parsimony is enhanced by naming nodes in cladograms.

4. Direction of evolutionary change is clarified the more derived species there are. The IRCI formula shows how additional derived species contribute to increased probability of a particular species being the ancestor of all derived species.

5. The greater the polarization among species of a group, the more support there is for one particular species being ancestor. The more derived (advanced or different) species of a group are, the greater the Bayes factors are.

6. Extreme polarization can justify an unknown shared ancestor or a new genus. When certain derived species are more similar to each other than to the ancestor, either an unknown intermediate shared ancestor can be postulated to minimize the amount of difference from the ancestor, or a new genus can be proposed based on that support.

7. Transformational radiation in the context of monophyly provides support for recognition of taxa. The minimum of two well-supported (7 dB) traits to establish serial transformation of taxa parallels a standard heuristic of systematics that it takes at least two traits for a species to be well distinguished.

Short decision tree for analysis

1. If none of the species in a clear-cut group have high probability of being the ancestral taxon, and the IRCI formula does not indicate that there is a high probability that at least one taxon is the descendant of another; then the direction of transformation is undecidable based on present data. Else …

2. If none of the species in a clear-cut group have high probability of being the ancestral taxon, and the IRCI formula demonstrates a high probability that one species is ancestral to at least one other; then the direction of evolutionary transformation is decidable. Given that there is no other group for these species, they all are descendants of that one ancestral species even based on present somewhat skimpy data. The species with highest probability may be identified as ancestral if it has a high enough Bayes factor when compared with the species with second-highest probability of being the ancestor. Else …

3. If one of the species has a probability higher than 0.95 that it is ancestral to the others, and the other taxa have lower probabilities that they, themselves, are ancestral to others; then, these probabilities are converted to Bayes factors, which can compare probabilities of hypotheses calculated from somewhat different data sets. An acceptably high Bayes factor (consult Table 2 in Part 2) confirms that one species as ancestral to the others. This is the ideal scenario. Else …

4. If two species have probabilities higher than 0.95 that they are the ancestral taxon of the group, which can happen because the data sets are different; then, a tentative decision may be made based on how much higher the deciban count is for the best candidate as ancestral species over that of the second best. This is similar to reliance on the Akaiki information criterion which gauges the amount of information lost if the second-best alternative is chosen.

Contrived Examples

1. Probability of being ancestral for species A is 0.70, for species B is 0.50, for species C is 0.30. The IRCI formula (from the spreadsheet available online, see Part 2) indicates that the chance of at least one of the three being ancestor of one of the other two is 0.90, which is marginally undecidable. Bayes factor for A being ancestral to B is 1.4, which by the table in Part 2 is trivial. (This is calculated as likelihood of A, or 0.70, divided by probability of B, or 0.50, which is 7/5, or 1.4.)

2. Probability of being ancestral for species A is 0.70, for species B 0.50, for species C 0.40, and for species D, 0.40. The IRCI formula gives these four species a 0.95 chance that at least one of them is ancestral to at least one of the others. The hypothesis is then decidable. Species A is an acceptable candidate for ancestral species but the Bayes factor for species A giving rise to B is only 1.4. Both species remain good candidates for ancestral status.

3. Probability of being ancestral for species A is 0.90, for species B 0.25, for species C 0.20, and for species D, 0.20. The IRCI formula gives these four species a 0.95 chance that at least one of them is ancestral to at least one of the others. The hypothesis is then decidable. Species A is probably the ancestral species because the Bayes factor for species A giving rise to B is 3.2, or substantial.

4. Probability of species A is 0.95, of species B is 0.30, of species C is 0.30, of species D is 0.20. The IRCI formula is unnecessary because one species is probabilistically the ancestral species. The Bayes factor of species A versus species B is 3.2, which is substantial and it may be considered ancestral.

5. Probability of species A is 0.99, of species B is 0.95, of species C is 0.30, of species D is 0.20. The Bayes factor for A being ancestral to B is 1.02, which is trivial. However, the number of decibans represented by clues for a probability of 0.97 is 20, while for 0.95 it is 13. The weight of evidence in spite of the low Bayes factor is clearly in favor of species A being ancestral to species B and therefore to the remainder of the species in the group. The amount of information lost would be 7 dB if the species B were chosen as ancestor.

Remember that the probabilities do not have to add to 1.00 because somewhat different data sets are being used, so there is no probability distribution contributed by species C and D to weigh against species A being ancestral to species B.

Bayesian priors are often a cause for concern, because it is often thought that they are guesswork that may adversely affect the result. They are assumed in deciban analysis, however, to be equivocal, or 0.50. Only likelihoods based on empiric data are then used to calculate Bayes factors.

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CLASSICAL DETERMINATION OF MONOPHYLY, EXEMPLIFIED WITH *DIDYMODON* S. LAT. (BRYOPHYTA). PART 2 OF 3, CONCEPTS

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ABSTRACT

Classical systematists infer evolutionary monophyly by using clues to adaptive or relatively neutral transformative radiation. If such clues are on a logarithmic scale they may be added to yield a probability for direction of evolution of one taxon to another. Such logarithmic clues are the decibans used by World War II code breakers in England. For a group, transformative traits are those convergent among disparate taxonomic groups, while conservative traits or trait combinations occur in multiple species and environments. Stem-based evolutionary trees (caulograms) are generated by models of serial evolutionary change. Direction of macroevolutionary transformation on a caulogram is determined by general morphological cladogram position, and maximum Bayes factor or deciban differential except when an intermediate taxon may be proposed, either from the extant set of terminal taxa or as an unknown shared ancestor that minimizes Bayes factor differences.

First, reassurance. This paper is mainly intended for classical taxonomists or the interested student. It attempts to explain what classical taxonomists do intuitively to generate evolutionary classifications. All relevant mathematics and statistics are simple and here thoroughly explained. Formalization in this paper means determining the statistical or logical basis for organizing related species according to increasing derivation away from some central apparently ancestral species. This paper is not primarily phylogenetic in that identification of shared homologous traits is only part of the method. This is because adaptive or relatively neutral, rare or unique, specialized, or otherwise divergent traits are also examined and evaluated in classical taxonomy to create predictive classifications. Suggestions are made here as to exactly how we use clues to direction of evolution in the taxonomic analytic and synthetic process. Prediction in evolutionary systematics involves placement in an evolutionary diagram that shows both shared ancestry and serial macroevolutionary derivation.

Second, definitions. Some terms appropriate for modern evolutionary systematics (Zander 2013) need a short explanation because of a different manner of use or because they are new.

- *Ancestor* in the present context is used for a taxon, as in "ancestral taxon," not an individual.
- *Bayes' Formula* is a simple statistical method of updating a previously accepted chance of something being true in light of additional information to provide a new ("posterior") probability of it being true. Sequential Bayes analysis simply uses a number of sets of data, one after the other, to continually update the degree of truth about something (such as a process in nature).
- *Clade* is a group consisting of an ancestor and all its descendants, and it is thus indicative of monophyly, but see Figs. 1, 2, 3 and 4.
- *Closed causal group* means that if one relationship is true between two elements, then the relationships of all the other elements are immediately deduced. That is, if one and only one species in a genus or infra group is determined to be the ancestral taxon for another in that

group, all the other species of the group must be also descendants, either immediate or secondarily, assuming again that this group has only one ancestral species.

- *Dissilient genus* refers to a group with a single generalized species with a cloud of clearly derived species associated with it. The derived species are more similar to the ancestral species than they are to each other. Some derived species (*stirps* sensu Zander 2013) may be so specialized as to appear to be dead ends in evolution, while others may prove advanced but generalist, capable of generating a number of specialized, derived species of their own and thus found a new genus.
- *Heterophyly* is either phylogenetic paraphyly or polyphyly, with the same taxon distant on a molecular cladogram and no other evidence of different origin or convergence. Heterophyly implies that intermediate cladogram nodes are of that same taxon.
- *Heuristic* is a short-cut or rule-of-thumb that provides an approximate answer sufficiently exact for everyday purposes.
- *Macroevolution* concerns taxa generating taxa, serially. This may be diagrammed with a *caulogram*, or stem-tree of both serial and branching relationships.
- *Superoptimization* is the process of intelligently assigning names to cladogram nodes — usually these are the names of exemplars or terminal taxa. Otherwise one may create a fully *natural key* (see example by Zander 2013: 80) involving such names, which may be holochotomous (serial/nested, one-branched), dichotomous, or polychotomous. Commonly, information that provides clues to direction of evolution is not phylogenetically informative (i.e., is not about shared ancestors).

Monophyly is determined by both shared ancestors and serial derivation of one taxon from another. Determination of monophyly through cladistic principles has been the object of thirty years of Hennigian phylogenetic analysis (Farris 2012; Felsenstein 2001; Pennisi 2003; Rieppel 2006; Vernon 1993; Williams 2012). Significant changes based on such have been made in classifications and in the way evolution is modeled. I have pointed out (Zander 2013) that phylogenetics cannot alone determine monophyly to any useful degree of accuracy. This is due to *apophenia*, seeing patterns in random data. In morphological cladograms, multiple descendants from one ancestral taxon may have some parallel traits, creating false synapomorphies, while reversals force a descendant lower in the cladogram. All this is due to the few expressed traits involved in speciation in any one part of a cladogram. In molecular studies, random survival of otherwise paraphyletic or phylogenetically polyphyletic molecular strains of the same ancestral taxon confounds interpretation of branch order of taxa. Non-phylogenetic information can correct phylogenetic apophenia to a large extent.

First, ask yourself if any of the taxa in a group qualify as ancestral to some or all of the rest of the taxa, ignoring the possibly misdirective cladogram. Divide your species into group of one potentially ancestral species and its associated derived species. This may seem foreign to students used to cladistic thought, i.e., "tree thinking," but one may imagine purposefully identifying a set of multifurcations. The Hennigian principle that of any three taxa of the same rank two are more closely related fails when the progenitor of both survives with expressed traits in stasis. A way to test this principle is to ask oneself if the group being studied is easily conceived as having one (or more) generalist species closely associated with a cloud of derived species more similar to the generalist species than to each other. If such multifurcations are seen as fundamental, then cladistic analysis is inappropriate, but evolutionary analysis remains possible. Relative stasis of the progenitor taxon is theoretically expected when the progenitor population is much larger than that of the descendants, in which case reduced rate of change by differential swamping of mutations can occur or there may be strong stabilizing selection (Haller & Hendry 2013; Pearman et al. 2007; but see Peterson et al. 1999). A recent, detailed, independent condemnation of Hennigian formalism was presented by Cavalier-Smith (2010).

Persistent molecular strains are implied by phylogenetic paraphyly. Molecular systematics assumes that molecular strains must quickly develop into new species when isolated. On the other hand, because non-coding and trivial genetic mutations occur and are fixed in both time and space, molecular strains are doubtless common. Isolated (in time or space or both) molecular strains of the same taxon may diverge with continued mutation of non-coding traits but without species level change in expressed traits. Abundant molecular paraphyly in cladograms of published phylogenetic papers demonstrates that surviving molecular strains of the same taxon may occur both before and after generation of one or more descendant species differing in expressed traits. Extinction of some molecular strains and survival of others in the same taxon implies that molecular cladogram nodes cannot be named with surety (Zander 2013: 51). In addition, there is lumping of taxa embedded in other taxa of the same rank in both morphological and molecular analyses, as "strict phylogenetic monophyly." Thus, monophyly is poorly discerned because branch order of taxa at any rank can be dubious. Although Mooi and Gill (2010) have contributed a recent, detailed, independent criticism of molecular systematics along similar lines, they make the mistake of assuming that "sequences of DNA and RNA are simply morphology writ small." The main problem is the false assignment of each molecular strain to separate taxa. There may be many parallel molecular strains somewhat distant on a cladogram because some have speciated, and many of these strains are extinct or unsampled.

Some phylogenetic methods are informative of evolutionary monophyly. Certain methods commonly used in phylogenetic analysis are acceptable as informative of serial ancestor-descendant relationships. Morphologically based cladistic analysis is a cluster analysis based on trait transformations, and as such has general utility, though limited by the stochastically based resolution of many groups of three or more species (or higher taxa) of which only one is surviving progenitor. Taxa in short or unitary lineages at the base of cladograms may be either advanced but with intermediate taxa extinct, or primitive (similar to ancient progenitors); but, if two or more such basal taxa are similar in morphology and also in different clades, their basal propinquity implies a primitive status relative to the taxa in the remainder of the cladogram (Zander 2013: 104, 165). Other than this information, a process of naming each node must be effected (parsimony through superoptimization) to collapse the OTU's into coherent progenitor-descendant groups (Zander 2013: 75).

Heterophyly in molecular cladograms is informative. Molecular analysis does reveal branching order of the molecular strains represented by exemplars because the molecular strains studied apparently do split in a dichotomous fashion and all are expected (or hoped) to have somewhat the same rates of mutation of tracking DNA bases. Because extinction or other non-sampling of molecular strains masks true progenitor-descendant relationships, the cladogram is restricted to branching order of the strains studied, which may grossly misrepresent species relationships. On the other hand, cladogram branches of strains of the same taxon that are distant on a cladogram do imply that the different taxa branching off between them are descendants of a deep progenitor of the taxon to which the distant strains belong. This heterophyly (paraphyly or phylogenetic polyphyly) is then informative of taxa that are in a serial ancestor-descendant relationship (Zander 2008) and do indicate what evolutionary direction (represented by changed expressed traits) that transformation took. A second value of molecular systematics is when two taxa are farther apart on a gene tree than expected by possible future informative heterophyly, such as strains of two species or two genera surprisingly occurring in two different families, at which time it may be concluded that there is no deep ancestral connection, and the two taxa are rightly separated. Using molecular heterophyly in determining order of serial taxic transformation is discussed in detail by Zander (2008, 2010a).

There are underlying bases for systematic analysis in addition to shared ancestry. Monophyly in classical systematics can be diagrammed as a caulogram (Besseyan cactus or caulogram) in which all parts of the evolutionary tree are named, if possible. The exception is when

two closely related taxa are each apparently characterized by equally advanced and specialized traits, and a shared ancestor may be postulated. The postulated shared ancestor minimizes credulity necessary for traits having apparent Dollo irreversibility as a group (i.e., macroevolutionarily, at the taxon level) (Atkinson et al. 2014; Gould 2002; Grant 1985: 329; Levinton 1988: 217). This paper is an attempt to formalize that process in classical systematics of intellectually and intuitively generating a caulogram from experiential data informed by process-based theory. Formalization to reveal underlying physical and statistical bases for systematic decision is important to justify credibility in scientific study using heuristics as opposed to the mechanical taxonomy associated with structuralism in phylogenetics (Zander 2010b). Of course, following Giere (2006), the "notions of reference and truth" developed for mathematics and physics may not be the only valid or practical guideposts to understanding a complex universe, but they suffice for this study.

Taxa evolve, not just traits. Many phylogenetic papers have deprecated standard evolutionary theory as contrary to cladistic results. Cladistic results are obtained by mapping of trait transformations on a morphological or molecular cladogram., that criticism is based the Hennigian fallacy, which is contrary to well-established theory (Bowler 1989: 346; Mayr 1981). This is in part because an algorithm expecting two of three taxa to be more closely related will in fact generate a fully resolved diagram by misinterpreting randomly congruent state changes as synapomorphies or a molecular strain as the complete taxon, when a multifurcation better represents macroevolutionary transformations. In fact, the opposite may be expected to be so in the majority of cases, that *immediate descendants, if two or more, will be more similar to their progenitor than to each other*. This last is a clear heuristic that I believe is much used in classical systematics. It is similar to the K statistic of Blomberg et al. (2003), but does not involve a measurement of phylogenetic signal. Sober (2008: 264) discussed at length the topic of shared ancestry, even invoking the Bayes formula to distinguish which hypothesis of Hennigian-style shared ancestry is more probable, but his rationale is throughout limited by a reliance on the Hennigian two-out-of-three principle.

Together with selected information from molecular and morphological cladistics, the modern heuristics of classical systematics can devise an acceptable caulogram that represents serial macroevolutionary transformations of monophyly. With formalization, the heuristics can be put on a mathematical and statistical methodological basis.

SERIAL MONOPHYLY VERSUS CLADES

Radiative evolution is the key to recognition of transformation of one taxon to another. When asking a classical taxonomist to estimate monophyly of a group in which he or she is expert, one can expect that taxonomist to sort and polarize the taxa into successive but also commonly branching groups each modified away from some central set of features identifiable as "general" or "primitive" for all taxa. Then each sub-group is evaluated as a kind of radiant circle away from a generalized ancestral taxon towards a set of often highly adaptive or at least neutral but unique descendants, representing radiative evolution into new environments, centrifugal from a generalized ancestral taxon. The result is a caulogram, or commagram, or Besseyan cactus. This sort of analysis is often done intuitively as a function of a mysterious facility of taxonomists called "expertise," not presently duplicable in software. Is there an intellectual structure to taxonomic expertise in determining serial monophyly? To what extent is experience a kind of frequentist statistic or generative of Bayesian expectation?

The classical systematist uses clues to both shared and serial relationships. Phylogenetics has formalized the grouping of taxa using clustering methods based on successive trait transformations, resulting in dichotomous trees of terminal taxa quite like standard cluster analysis but with more information beyond raw or massaged similarity. Each node in a cladogram represents the beginning of a supposed monophyletic group, called a *clade*. Tree-thinking methods are criticized

at length in "Framework for Post-Phylogenetic Systematics" (Zander 2013), and a caulistic (stem-thinking) alternative to cladistics is there proposed. The use of heuristics in classical systematics was treated (Zander 2013), but only one aspect was *formalized* (i.e., given a clear physical or mathematical structure or explanation), namely, the geometric mean basis for the paradigm (a–)b–c(–d) in descriptive measurements.

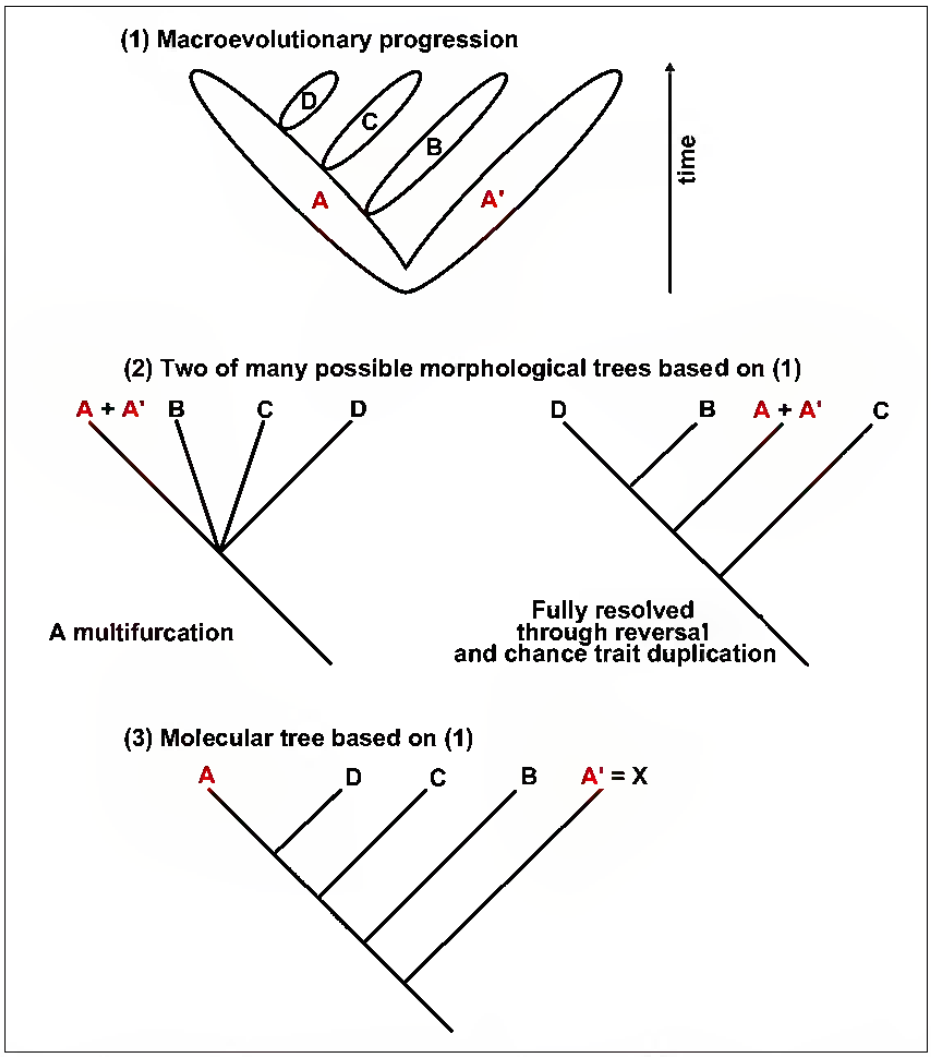

Figure 1. Comparison of contrived trees of the same evolutionary scenario. **(1)** Macroevolutionary progression of three derived species B, C and D, in that order, from species A. Species A has previously split into two isolated but morphologically static and identical populations, A and A'. **(2)** Cladograms of parsimonious analysis of morphological traits. Left is a multifurcation. Right is a fully resolved morphological cladogram with chance duplication of traits in B and D, and reversal of a trait in C. **(3)** Molecular tree showing A as terminal having generated B, C and D in the past while itself mutating but A' is treated as a new cryptic species "x".

Cladistic analysis is accepted as valuable for preliminary clustering of taxa, but it must be carefully evaluated because the central Hennigian thesis that of every three taxa two *must* be more closely related can be quite wrong for estimated order of branch splitting. In the present paper, the ability of classical systematists to evaluate evolutionary monophyly intuitively is examined and

formalized as actually a combination of cladistic-style evaluation of shared conservative tracking traits and a simple sequential Bayes analysis (explained by Kachiashvili 2012) done through assignment of coarse likelihoods as clues in the manner of World War Two code breakers.

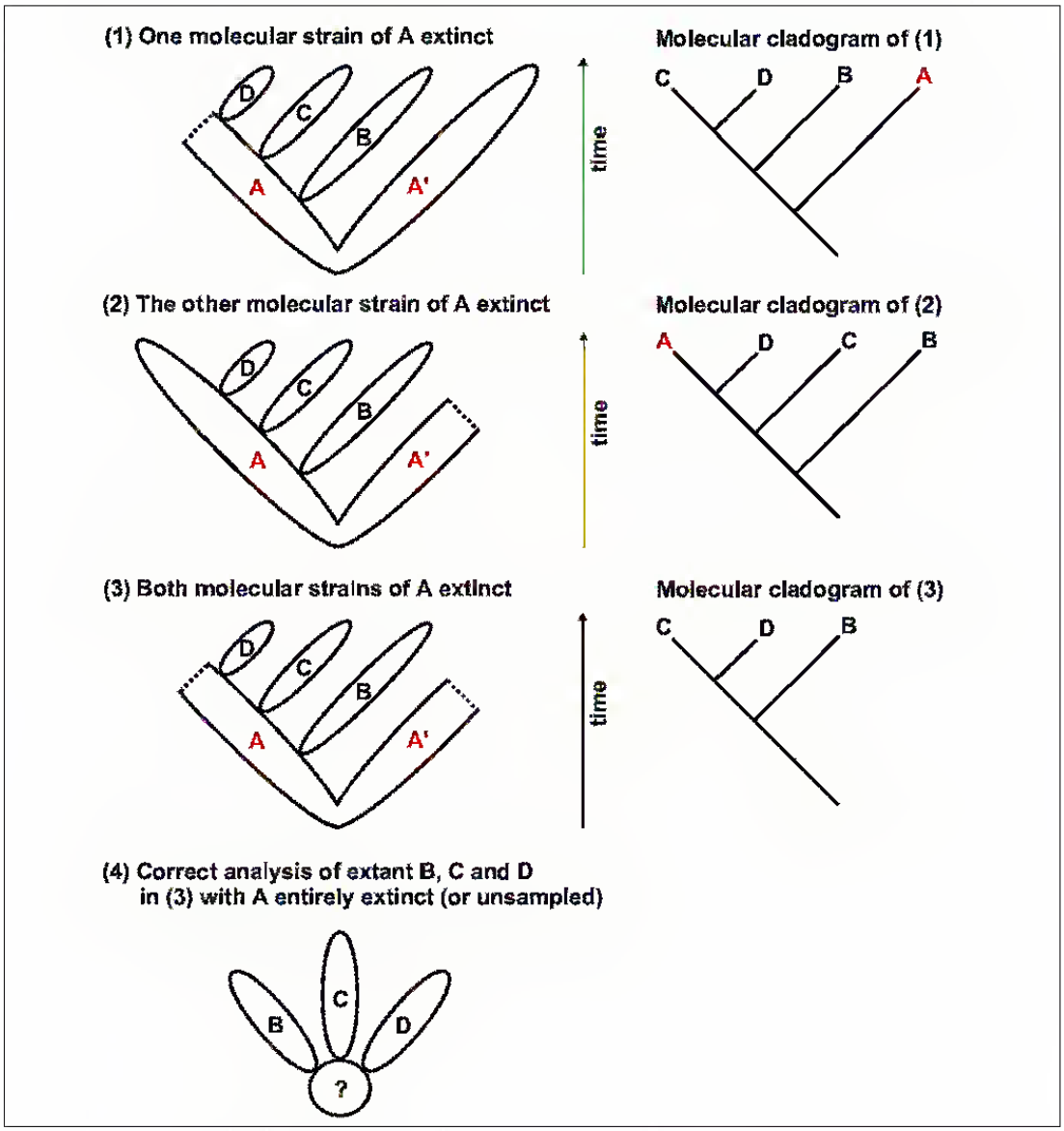

Figure 2. Effect of extinction (or non-sampling) of molecular strains of ancestral species. **(1)** A (one of the ancestral molecular strains) is missing, molecular cladogram at right has species A basal. **(2)** A′ (the other ancestral strain) is missing, species A is terminal. **(3)** Both molecular strains of species A are missing, and molecular cladogram is restricted to B, D, and D. **(4)** This is the correct caulogram for the extinct ancestor and its descendants (3).

ILLUSTRATED COMPARISON OF CAULOGRAMS AND CLADOGRAMS

It is untrue that two of every three taxa must be more closely related. After thirty years of viewing evolutionary relationships diagrammed with cladograms, the reader may find difficulty assimilating a way of presenting both serial and lateral evolutionary relationships, the caulogram (also known as the Besseyan or Bessey's cactus). The restriction of cladograms to showing shared

ancestry alone can bias the presentation of information in various ways. Such differences need explication, which is given here in a series of illustrations (Figs. 1–4).

Figure 1 is an exemplary analysis comparing various contrived trees of the same evolutionary scenario.

Figure 1(1): macroevolutionary progression of three derived species B, C and D, in that order, from species A. The last previously split into two isolated but morphologically static populations, A and A′. Note the time bar on the right. This is a caulogram.

Figure 1(2): shows cladograms of parsimonious analysis of morphological traits. Left is a multifurcation as expected if traits of derived species did not reverse or duplicate. A and A′ are correctly treated as the same. On right is a fully resolved morphological cladogram with chance duplication of traits in B and D, and reversal of a trait in C. All three species, B, C and D, remain derived from A, however, no matter where on the cladogram they appear.

Figure 1(3): presents a molecular tree showing A as terminal having generated B, C and D in the past while itself mutating (a "self-nesting tree"), but A′ is treated by molecular phylogeneticists as a new cryptic species "x". Although (2) and (3) show cladistic (lateral) relationships they are wrong because the serial relationship is ignored. Note no time bars for (2) and (3). The macroevolutionary formula for all three, (1), (2) and (3), is (A, A′) > ^{1}B, ^{2}C, ^{3}D.

Figure 2 shows effect of extinction (or non-sampling) of molecular strains of ancestral species.

Figure 2(1): A (an ancestral molecular strain) to be missing, and molecular cladogram at left has species A basal.

Figure 2(2): A′ (non-ancestral strain) is missing, species A is terminal. Given that only one molecular strain of species A is known, the macroevolutionary formula is A > ^{1}B, ^{2}C, ^{3}D for both (1) and (2) yet the molecular cladograms are not congruent.

Figure 2(3): Both molecular strains of species A are missing, and the molecular cladogram is restricted to B, D, and D. It is fully resolved although from other information B, C and D are apparently equally derived from some unknown ancestral species.

Figure 2(4): This is the correct caulogram for (3). Only when there is no known candidate ancestral species for two or more equally derived species can an unknown shared ancestor be postulated.

Figure 3 asks the question that given that we do not know the true macroevolutionary relationships, what is the best we can do in determining branch order? This figure shows what we can infer from minimal data on a molecular tree. Remember that the ancestral nature of A and derived natures of B and C are determined in large part in superoptimization by non-phylogenetic (non-shared ancestry) information. Even this basic information, however, is not available from the phylogenetic molecular analysis of *Didymodon* s.lat. by Werner et al. (2005) because the segregate genera are scattered and in very short branches (Zander 2013: 89–90). But if such information were available for the contrived example in Fig. 3, then:

Figure 3(1) Heterophyly implies that B and C are derived from species A, and the more terminal of the two is last in order of speciation, e.g. (A, A′) > ^{1}C, ^{2}B

Figure 3(2) If a species judged ancestral by non-phylogenetic information is terminal, species clearly derived from it are in order, e.g., A > ^{1}C, ^{2}B

Figure 3(3) If only two derived species are more terminal than the ancestral species, no order is discoverable because they are presented as sister groups. Thus, A > B, C

Figure 3(4) But if three or more derived species are more terminal, the lowermost are in discernable order, e.g., A > ^{1}D, ^{2}E, ^{3}F, ^{4}(C, D)

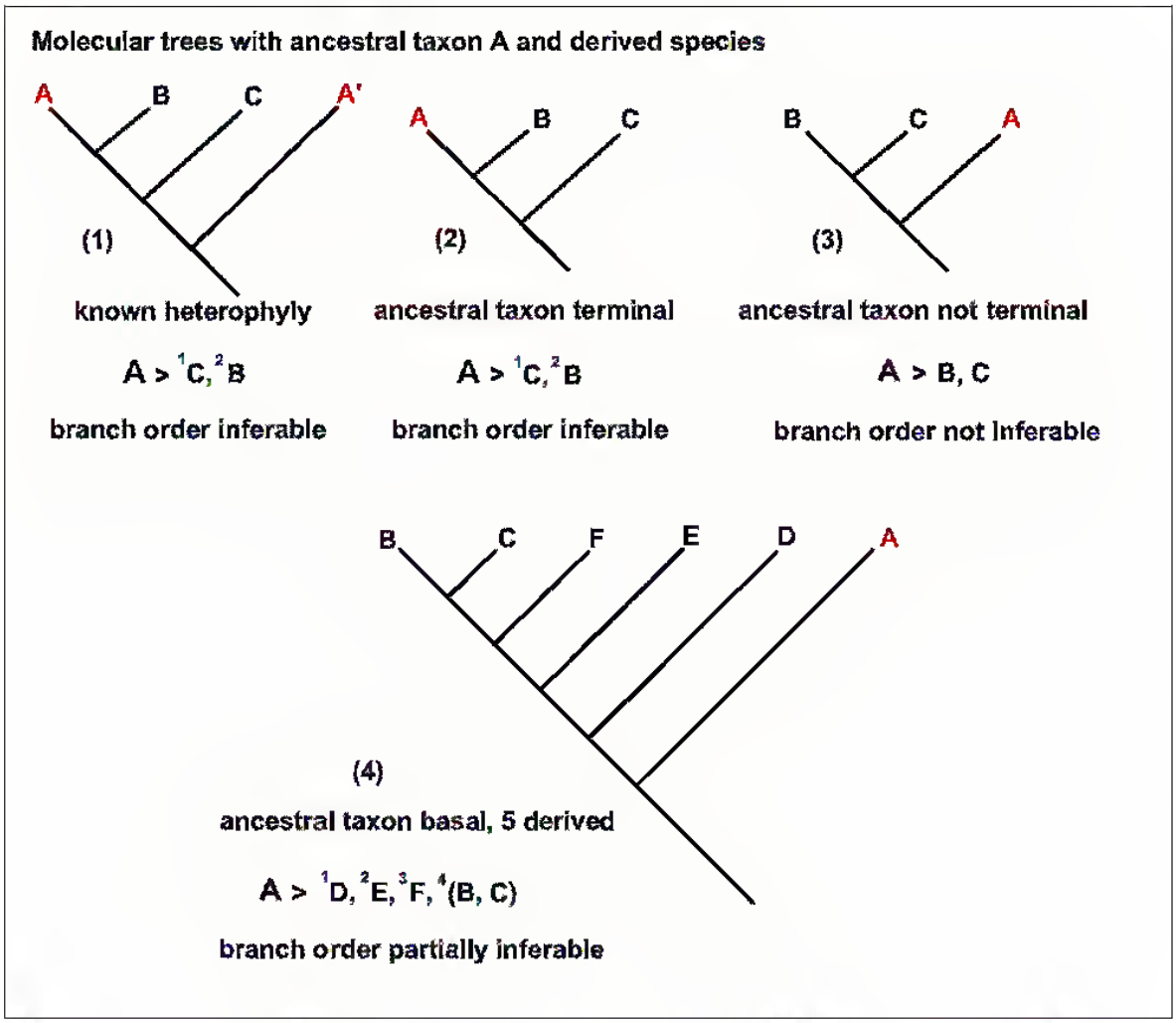

Figure 3. Inference from minimal data on a molecular tree. **(1)** Heterophyly implies that B and C are derived from species A, and the more terminal of the two is last in order of speciation, e.g. (A, A′) > ^{1}C, ^{2}B. **(2)** If a species judged ancestral by non-phylogenetic information is terminal, species clearly derived from it by non-phylogenetic information are in order. **(3)** If only two derived species are more terminal than the ancestral species, no order is discoverable because they are presented as sister groups. **(4)** But if three or more clearly derived species are more terminal, the lowermost are in discernable order.

Figure 4 explains how the principle of strict phylogenetic monophyly does not reflect generation of a taxon of higher rank from another. Genusation, for example, is generation of a new genus from a species in another genus, or just from the other genus if which species is ancestral cannot be readily determined. Can you see the two genera in Fig. 4? Both species A and B generate derived species based on superoptimization information evaluating ancestral and derived species. B, like A, is identifiable as central to a particular dissilient (exploding) genus concept. The macroevolutionary formula of this caulogram is (**A**, A') > ^{1}(**B** > ^{1}E, ^{2}F, ^{3}G), ^{2}C, ^{3}D. In this contrived example, we know both serial evolutionary direction and the branch order. In practice, the formula is usually incomplete.

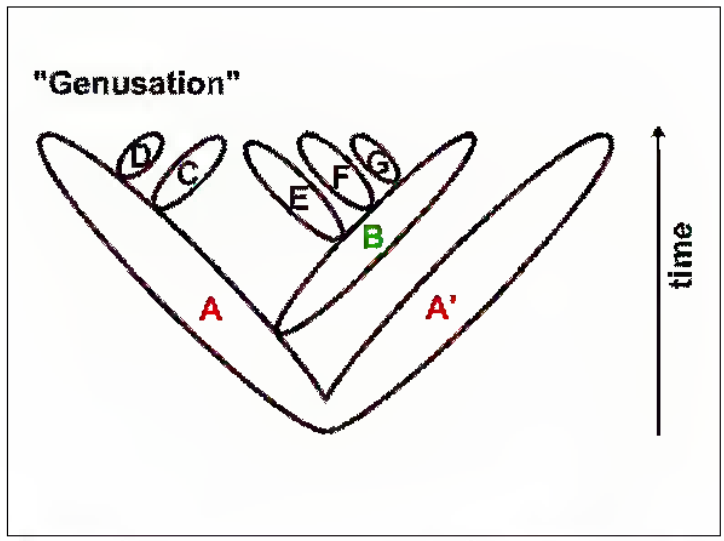

Figure 4. Genusation is generation of a new genus from a species in another genus. Can you see the two genera in Fig. 4? B, like A, is identifiable as a species central to a particular dissilient (exploding) genus concept.

Convergence analysis

Evolutionary stasis of ancestral taxa does not mean they do not speciate. That progenitor-descendant series exist and are often abundant is demonstrable in the evolutionary literature, and in the associated phenomenon of phylogenetic paraphyly in both morphological and molecular analyses. If any population is split and isolated in two or more unequal parts (e.g., peripatric speciation, see Futuyma 2009: 484), including founder events, genetic stability through time is expected to be greater in the larger portion. It is commonly acknowledged that allopatric speciation (Futuyma 2009: 472) is quite common or even more common than sympatric (Barraclough & Nee 2001, Mayr 1954, 2001). Species may remain static for millions of years, whether of large distribution or not, but smaller or founder isolates (including sympatric isolates) may speciate rapidly, escaping the homogenizing effects of gene flow, and more rapidly drifting in traits or changing through selection (Via 2001). There is great evidence from fossil studies that stasis in expressed traits (Haller & Hendry 2013) associated with punctuated evolution is common (Benton & Pearson 2001). Surviving progenitor species with two or more immediate descendant species are to be expected.

Recognition of the difference between generalized ancestral taxa and specialized descendant taxa is often easy for an expert in the group. The phylogenetically assumed pseudoextinction (rapid post-speciation anagenetic change on the part of a progenitor species) is thus theoretically uncommon. Figure 2(4) shows similar branching from an unknown shared ancestor but the ancestor may be pseudoextinct or simply unsampled. For evolutionary science to advance, theory

is used to create models to explain process-wise the relationships of organisms. By evaluating sets of closely related species, experienced taxonomists can usually identify a surviving progenitor from its surviving descendants by reference to rules of thumb (heuristics) that are widely accepted. *Convergence analysis* is simply the heuristic that if a trait (or set of traits) is scattered about an accepted classification, these are convergent (or parallel if from the same ancestral taxon), and are therefore may be either radiatively adaptive or are at least an element in transformation away from a generalized species.

There are well-established clues to direction of evolutionary radiation. Progenitors are taken here to generally have comparatively broad distributions, occur in older habitats, occupy less specialized niches, are morphologically generalized, have all expressed features (are not much reduced), are polymorphic with many subspecies, varieties, biotypes or cytotypes, have a distinctive morphological trait combination that may be variously modified or reduced, and lack asexual reproduction as primary. In the present paper the likelihoods are clues about direction of evolutionary transformation along the lines delineated by Grant (1949), Simpson (1953) and Mayr (1954) in the context of the New Synthesis, and of others who have discussed adaptive trends and orientations in detail (e.g., Futuyma 2009: 595; Gavrilets & Vose 2005; Seehausen 2006). According to Schluter (2000: 2), "Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It occurs when a single ancestor diverges into a host of species that use a variety of environments and that differ in traits used to exploit those environments." It is possible that some new traits associated with radiation are not adaptive (Gittenberger 1991; Gould & Lewontin 1979; Rundel & Price 2009), so one should identify putative descendants as simply transformative radiation, including both changes associated with adaptive radiation and new neutral traits whether refractory to selective pressures or not.

Convergence is a clue to adaptability of traits. Neutral morphological traits are only neutral as evolutionarily "local" conservative traits. According to Simpson (1953: 174, 179) conservative traits almost always are have adaptive significance for higher categories. Adaptive traits, if identifiable, might thus be informative of direction of macroevolution. They converge across taxonomic boundaries as different taxa adapt to the same evolutionary pressures. Conservative traits do not converge except at high taxonomic levels when associated with phyletic constraint, and are not immediately informative at the species level. Convergence analysis distinguishes adaptive from conservative traits and weights adaptive traits by level of confidence in distinguishing direction of evolution.

There are two principles of convergence analysis in the present paper.

First is that **for any closely related group, taxa with advanced specialized traits have a more generalized taxon as shared ancestor**. Thus, a possible dead end will have an entrance somewhere. Such a generalized ancestral taxon may be extinct or simply unknown but it can be "described" (and searched for) as at least having the common traits of the remaining species. Given this method of analysis, monophyly with named or at least describable ancestral taxa is possible. This can replace the "clade" of phylogenetics in which every node is necessarily an unnamed and unnamable ancestor of ultimately all distal branches, which is palpably incorrect because many nodes are easily named and many of these are of the same taxon (Zander 2008).

Second, **post-dissilience descendant-descendant transformation series with no reversals are preferred**. That is, after an ancestral taxon has generated a set of descendants, those descendants may be expected to telescope outwards (nest) by generating descendants of their own with increasing specializations. Sometimes, a new generalized taxon of higher rank may be a descendant (Fig. 4). Takhtajan (1997: 4) emphasizes this point: "Every new stage of evolution, and consequently every new taxon, differs from the ancestral taxon by an acquisition of some new, derived characters. The

ancestral taxon, on the other hand, will differ from its descendants by the absence of these derived characters." The simplest case is when no reversals are required and the putative secondary descendant is simply a sub-set of its immediate secondarily progenitor species (see discussion of *Vinealobryum brachyphyllum* and *V. nevadense,* and of *Geheebia fallax, G. ferruginea, G. maxima,* and *G. gigantea*, below).

Conservative traits may be weighted by the number of different habitats they tolerate. The transformation from one genus to another theoretically involves fixation of a *set* of different conservative traits in the progenitor that occur in a multiplicity of somewhat different environments. Phyletic constraint (restriction of a taxon to environments survivable with that set of conservative traits) both restrains the increase in number of conservative traits and the survival of organisms without the full complement. Thus, existence of at least one generalized species in a genus demonstrates long-term (multiple speciation events) survival of that conservative trait combination in the most ideal of environments. Conservative traits, as is the case with non-coding or genetically trivial DNA bases, can thus be used to track evolution.

Conservative traits are those refractory to selection because they are in combination evolutionarily neutral or neutral enough for that group in its particular range of environments given phylogenetic constraint of other expressed traits. They are identified as those tolerating a range of selective regimes. Such can be judged by the number of species of a group in which the traits occur, given that each species has or probably has a distinctive adaptive range. Thus, cladistic logic works fine to cluster conservative traits that track evolution, yet fails when highly adaptive traits are automatically assigned synapomorphy status simply because they appear in two or more species that morphological and ecological evaluation may deem more probably all joint descendants of one other generalized species. The present analysis began with a cladistic (Zander 1998, 2001) study of *Didymodon* Hedw., a genus of mosses (Bryophyte, Pottiaceae) that used equal weighting of traits but happened to matched past classical groupings (Zander 1993).

Adaptive or transformative radiation is considered a standard view of macroevolutionary change, is implicit in classical systematics (e.g., generation of a caulogram or Besseyan cactus), and comprises the data used in classical heuristics relating to monophyly. This paper studies the backbone of those heuristics, namely the mathematical and statistical structure that allows evaluation of the significance of the data.

The equivalent of Hennigian pseudoextinction is possible, but probably rare. Dichogamy (equal splitting and isolation of a progenitor population) may give rise to two descendants that gradually diverge. This is equivalent to Hennigian pseudoextinction. Another equivalent is extinction of ancestral species or those of intermediate morphology such that two species are so different but equally specialized as to be equivocal in estimation of a serial transformation series. Both scenarios must be included in estimation of progenitor-descendant series and signaled as involving an unknown shared ancestor, but there should be a justification based on process-based evolutionary theory, not an axiom for reliance on cladistic splits.

DETECTIVE WORK IN CRYPTANALYSIS

Sequential Bayesian analysis is a powerful tool. This paper makes use of sequential Bayesian analysis. The essence of Bayesian analysis is to combine a prior (chance of the hypothesis given prior knowledge) with a likelihood (chance of the data given the hypothesis) to calculate with the Bayes Formula a posterior probability (chance of the hypothesis given the data and the prior). Details of Bayesian analysis as used in phylogenetic analysis is presented well by Sinsheimer et al. (2003) and by others, and will not be discussed here. Kruschke (2011) has recently produced a

software-oriented (R and BUGS) manual for Bayesian analysis that is potentially highly flexible although the de novo programming of a MrBayes equivalent would be daunting and superfluous.

Sequential Bayesian analysis was developed by A. Wald and others (Kachiashvili 2012; Wald 1947), and was kept secret by the United States because of its value during World War 2. About the same time, it was separately developed in Britain by Alan Turing, in a somewhat different form. Again, applications to the British war effort and later the Cold War kept it secret until about 1980 (Good 1979). It is a form of empiric Bayes (McGrayne 2011: 134, 168, 205)—the posterior probability that was obtained from the first calculation is used as the prior for a second Bayesian calculation with another additional likelihood from additional data, and so on with added data until a stopping rule is triggered or one runs out of data. A formal equation for Bayesian causal induction involving a stopping rule is given by Bonawitz et al. (2013), but amount of data, in the present study, is the limiting feature. The assumption is that the shape of the distribution curve for the data of each sequential implementation is the same, i.e., conjugate priors (McGrayne 2011: 149).

Sequential Bayesian analysis is increasingly used with sequential sampling, but it may also be used when dealing with individual "particles" of information. When the data change with time, this quasi-recursive method is known as Sequential Bayesian Updating (Lauritzen 2009) and is used for control in robotics, speech recognition, political polling, target tracking, and steering/control, for example of large ships, airplanes, and space ships. In taxonomy, it has been examined as a method for identification of bacteria (Gyllenberg & Koski 2002), but that paper is largely of mathematical proofs of certain very general assumptions. The heuristic use of sequential Bayesan analysis (as "updating") in day-to-day human affairs was investigated by Bonawitz et al. (2013). They found that a simple Win-Stay, Lose-Shift sampling algorithm, in which a learner keeps a particular hypothesis until receiving evidence that is inconsistent with the hypothesis, approximates Bayesian inference, and does so efficiently. Sequential Bayesian analysis in the present paper is suggested as a formal, previously unrecognized basis for heuristic evaluation of monophyly in classical systematics.

Adding decibans together may be used as a substitute for using Bayes' formula. Alan Turing's work in breaking German war codes during the 1940's (McGrayne 2014: 67) led to his use of a kind of sequential Bayesian analysis. Given that computers were then primitive, being hand-operated, logarithms were extensively relied on. Turing, with I. J. Good and others in the group of code breakers at Bletchley Park, used clues, often tiny clues, to narrow down particular settings of the Enigma machines the Germans used. Statistically, the unit they used was the ban, which indicates that one hypothesis is 10 times as likely as an alternative hypothesis. The basic unit for a clue was the deciban (abbreviated dB), defined casually as the minimal level quantifiable as a measure of belief in a hypothesis, somewhat more precisely as an change in odds ratio from 1:1 to about 5:4. (Remember that an odds ratio of, say, 2:1 is actually the fraction 2/3, where the denominator must be increased by the value of the numerator. The odds ratio of 1:1 is 1/2, and 5:4 is 5/9.)

A deciban is technically 10 times the base 10 log of the odds, or $10^{n/10}$:1, or a ratio of tenths of a power of 10 to one. It is a logarithmic unit of probability that measures information (or entropy). It is a decimal digit as opposed to a bit, which is a binary digit. One ban corresponds to about 3.32 bits, and a deciban is about 0.33 bits. A change of 1 deciban changes the odds by a factor of approximately 5:4. A change of 10 decibans changes the odds by a factor of 10, 20 decibans changes the odds by a factor of 100. Most systematic analysis is restricted to a range of 1 to 20 decibans (0.55 to 0.99 probability values), whether given as exact or informal probabilities.

Turing and his group found that by combining clues (some in hundredths of a deciban) enough relevant information could be gathered together to break codes. The process was essentially Bayesian, and can be easily matched using today's computational conveniences (e.g., a spreadsheet as

discussed below) with sequential Bayes calculation. In fact, the probabilities associated with decibans are exactly duplicated by sequential Bayes analysis. To review the equivalencies, an *odds ratio* of approximately 5:4 is equal to the *fraction* 5/(4+5), and that is the decimal fraction 0.05555..., an approximation of one deciban. The exact deciban calculation of $10^{n/10}$:1 as odds ratio is equal to the fraction $10^{1/10}/(10^{1/10}+1)$, which is the decimal fraction 0.5573.... With a prior of 0.50 and a likelihood of $10^{1/10}/(10^{1/10}+1)$, the Bayesian posterior probability is the exact same decimal fraction 0.5573.... If one does have posterior probabilities that include priors that are not 0.50, then convert by multiplying by the reciprocal of the priors (Kruschke 2011: 253), but this is not necessary with deciban calculations.

Using decibans does not require computers. Two and five decibans add (logarithmically, as with a slide rule) to seven decibans, and from the formula $10^{7/10}/(10^{7/10}+1)$ we get the decimal probability 0.8337...., which can also be read off a chart (see Table 1). Bayesian sequential analysis with a spreadsheet yields the same results, with more complex but more flexible calculation. With a prior of 0.50 and seven likelihoods of $10^{1/10}/(10^{1/10}+1)$ each of the seven being analyzed with sequential Bayes (using each posterior as the prior of the next calculation), the same decimal 0.8337 is also obtained. Clearly, using decibans is a short cut in Bayesian sequential analysis and can have heuristic value as a simplifying tool.

CLADOGRAM ERROR

The resolution of molecular trees of branch order of taxa is not high even if branch order of molecular strains is well determined. In phylogenetics, each node defines the start of a clade. Yet in morphological cladograms, chance matching of new traits during parallel speciation from one ancestral taxon results in false synapomorphies, thus false nodes. In molecular cladograms, the potential for hidden paraphyly (or heterophyly) caused by extinct or unsampled molecular strains, and for generation of multiple descendants from one ancestral taxon makes any node uncertain as to whether or not it is the beginning of a clade.

If any molecular analysis is liable to uncertainty because of the above potential problems, one cannot use details of the analysis for classification purposes. The branch order resolution of a molecular cladogram cannot be better than the average distance of known heterophyly. One might expect an average resolution of at least three or four nodes for widespread taxa and often up to 10 nodes for certain taxa (e.g., *Brachyglottis, Ligularia* and *Senecio* in Senecioneae, Asteroideae, Pelser et al. 2007). This applies to any rank exhibiting paraphyly, species, genus, or family. Of course there is a limit to uncertainty due to expectation of hidden heterophyly, since one might not expect it to cross established higher ranks.

If known molecular heterophyly is largely, say, two nodes, as modeled in Figure 5, then an error bar showing this uncertainty might be inserted for each phylogenetically postulated "shared ancestor." All postulated shared ancestors are then affected by overlapping error bars, see Fig. 5(1). Molecular heterophyly as in Fig. 5(2) and superoptimization as in Fig. 5(3) largely eliminate uncertainty due to paraphyly. Note in Fig. 5(3), even though nodes with known ancestral taxa crowd the end of the cladogram, the error bars remain and represent predictive uncertainty for any new taxa that might be inserted into the cladogram. Such a problem is obviated if new taxa are inserted into the equivalent caulogram of Fig. 5(4), which is why caulograms are ultimately better than cladograms.

Why such an involved and complicated introduction? Lakatos (1978) proposed that research papers do not need a justification of their theoretical basis for each publication in those cases when a firmly established intra-disciplinary research program is understood. Even if the researcher is not fully familiar with every theoretical nuance, a paper observing standard protocols indeed contributes to science. In systematics, for instance, a paper that is simply a check list of species for

an area is accepted as part of a 250-year research program documenting and explaining when possible the historical biogeography of the earth's life. The present taxonomic paper requires a detailed theoretical justification, however, because the appropriate research program is new, and is, in Lakatos' sense, progressive in predicting novel facts. Besides, although the human brain is slow to work out complex problems, its own complexity and power can deal with that complexity, slowly but surely.

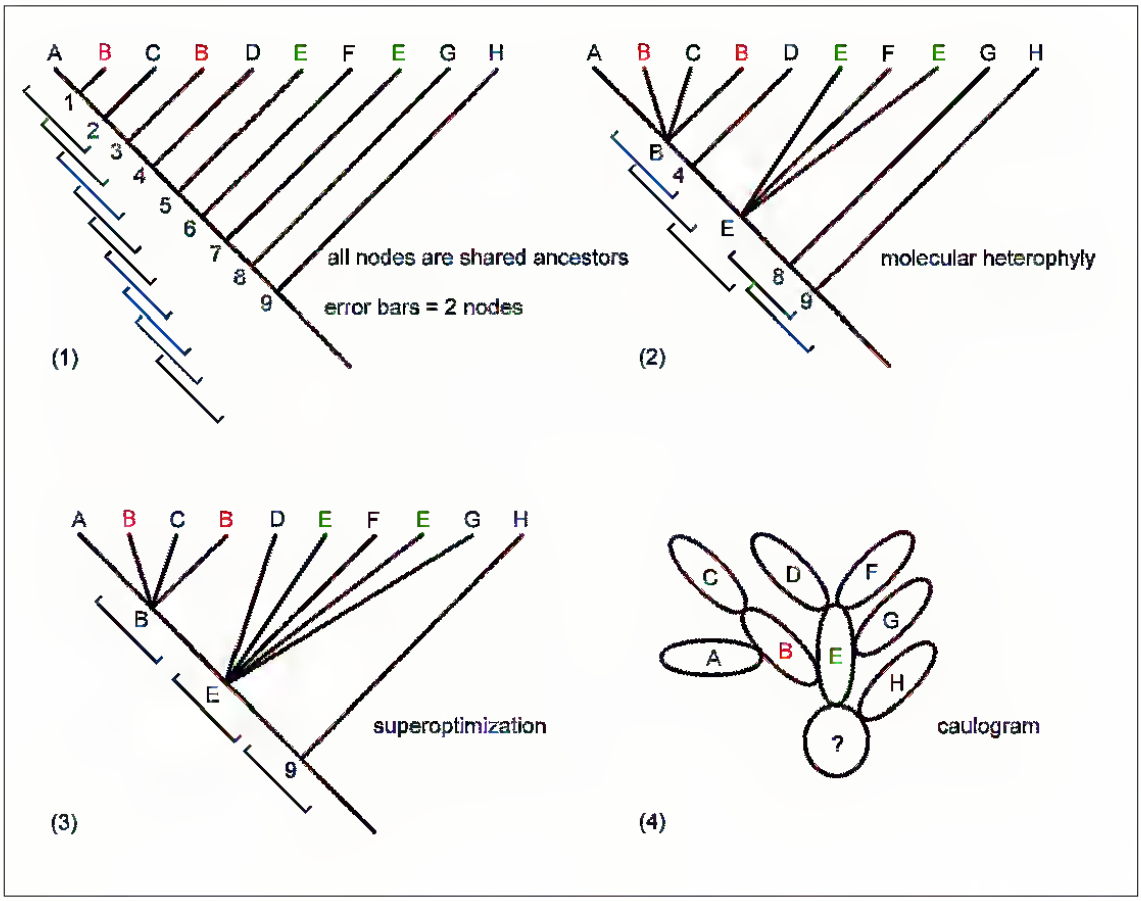

Figure 5. Analysis leading to a caulogram, based on a terminal portion of a molecular cladogram. Heterophyletic terminal exemplars (of species B and E) are in color, they are of the same taxon but each distant by two nodes. (1) Overlapping error bars for all nodes when all are each treated as a shared ancestor. (2) Molecular heterophyly eliminates much uncertainty by identifying one taxon giving rise to another. (3) Superoptimization through identification of ancestor-descendant relationships on the basis of non-phylogenetic information reduces uncertainty more. Node 9 in this contrived example cannot be eliminated because exemplar H cannot be easily assigned in this example to an extant group, and remains an unknown shared ancestor. (4) Caulogram showing stem relationships.

METHODS

PROBABILITIES AND SUPEROPTIMIZATION

Simplifying formal estimation of probabilities uses decibans. Probability is here not just expected intersubjective agreement, but also a measure of how much more predictive or explanatory one model is over another. Informally, the probability imbued in a scientific hypothesis must be tested by real decisions and their aftermath. Classifications are the result of series of heuristic

decisions over time (250 years of Linnaean and 150 of Darwinian taxonomy), much like updating in sequential analysis. Formalization involves assigning probabilities as measures of expectation on the basis of theory; these are coarse measures, but nonetheless not "mere" intuition. There are four ways probability is used in this paper: (1) Sequential Bayes analysis of "clues" to direction of serial transformation using decibans and perceived radiative transformations is done in much the same spirit as by code breakers during the Second World War. (2) Bayes factors are used to evaluate competing hypotheses. (3) Probability that at least one ancestor-descendant transformation is correct (IRCI formula below) uses the concept of a closed causal pool. (4) Deciban differentials allow distinction of the two most likely models when the B.F. of each are very close. The calculations in this paper use simple mathematical concepts suitable for traditionally innumerate taxonomists, and are facilitated by spreadsheets available online at <http://www.mobot.org/plantscience/resbot/evsy/sprsh/>. The spreadsheets can be "unprotected" and modified for use with larger numbers of traits and taxa.

Intuitive expert systems can be explained. The analysis of serial macroevolutionary transformations at the taxon level was discussed at length by Zander (2013). In the present paper, an expert system is exemplified that attempts to formalize (identify physical and mathematical bases of) the scientific intuition approach referred to in the past as Gestalt or omnispection methods. Two data sets are gathered for the group studied, one set for shared traits published by Zander (1998), and another set (see tables in Part 3) for unique and apparently advanced traits. The first set is of homologous traits that may be used in cladistic analysis, the second largely of autapomorphies.

"Superoptimization" means naming cladogram nodes to eliminate invention of unknown shared ancestors. The deeper a taxon is buried in a rooted cladogram (subtended by many nodes) the more likely it is to be advanced in terms of serial transformation, but this is usually masked to a great extent by false resolution due to a methodological requirement that of every three taxa, two are more closely related, resulting in branch order based on chance (parallel) shared traits or reversed traits. This problem is resolved by "superoptimization" (Zander 2013: 75), which is the naming, whenever possible of cladogram nodes. This results in identification of groups of one progenitor taxon and one or more immediate or secondarily descendant taxa. This is usually done informally in classical taxonomy, through omnispection and reliance of a set of informal heuristics that identify primitive-advanced transformations along the lines of evolutionary theory.

This has already been done for *Didymodon* by Zander (2013: 80). That same analysis is continued in this paper but with formalization of the heuristic used in superoptimization. The intuitively superoptimized groups are here re-analyzed by assigning each taxon a set of clues or items of evidence. A dissilient genus (Zander 2013: 83, 92) is often easily identified as a group of similar species with a putative ancestral taxon for the other species. Inasmuch as nature teaches us taxonomic concepts, there may be other definitions of taxonomic groups that are equally effective in prediction when dissilience is not evident. The putative progenitor has a maximum of theoretically primitive (i.e., first of a series) traits vis-à-vis those of the other taxa in the group.

One can assign one deciban as minimal clue, or a higher number of decibans for very convincing clues. With sequential Bayes analysis, with all evidence treated as minimal clues (0.56 probability) and assuming an initial 0.50 prior, 13 Bayesian operations (13 clues, that is, 13 likelihoods) are needed to provide minimal scientifically reliable support (0.95 or more). A single 0.76 (5 dB) likelihood among the sequence reduces the number of clues needed to eight for scientific reliability. Two 0.76 likelihoods reduces the number of clues needed to four. Thus, moderately strong evidence, if convincing, can be quite helpful in supporting a particular hypothesis. With strong evidence, three Bayesian operations at 0.76 (5 dB) likelihood surpass a standard scientific minimum 0.95 at 0.97; four at 0.76 likelihood gives 0.99. Thus, three clues determined to be of moderate not minimal import (0.76) can combine in sequential Bayes analysis (with an initial 0.50 prior) to yield a

scientific minimum reliability for whatever hypothesis is examined, four giving very strong scientific support. Coarseness in assignment of clues to direction of macroevolutionary transformation aids in making these studies repeatable, using, say, only odd numbers of decibans (1, 3, 5, 7) as is done here.

Deciban analysis is like using a slide rule. Table 1 compares the probabilities of evolutionary serial transformation using decibans obtained from numbers of perceived advanced transformative traits. The probabilities are given from 26 to −26 dB because negative decibans are required when evaluating pro and con hypotheses; zero decibans is 0.50 probability. Figure 6 presents a chart of the exact probabilities on the y-axis, and decibans on the (logarithmic) x-axis. A dashed horizontal line is given for 0.95, 0.99, 0.76, 0.56 and 0.50 probabilities, showing their position on the asymptote. Their negative values are also given for dB less than zero (i.e., less than 0.50). One can use this chart for quick estimation of probabilities. Three clues in a sequential Bayesian analysis can be read off the 3 dB bar. Two clues of one deciban each plus one element of moderate support of five decibans adds to seven decibans, or 0.833 posterior probability for that single analysis of the probability that a taxon was derived from another. Note that this method is similar to the use of the logarithmic scales on an analog slide rule. Dealing with complex digital calculation through the mental analogue of a specialized slide rule may partially constitute "intuition" in systematics.

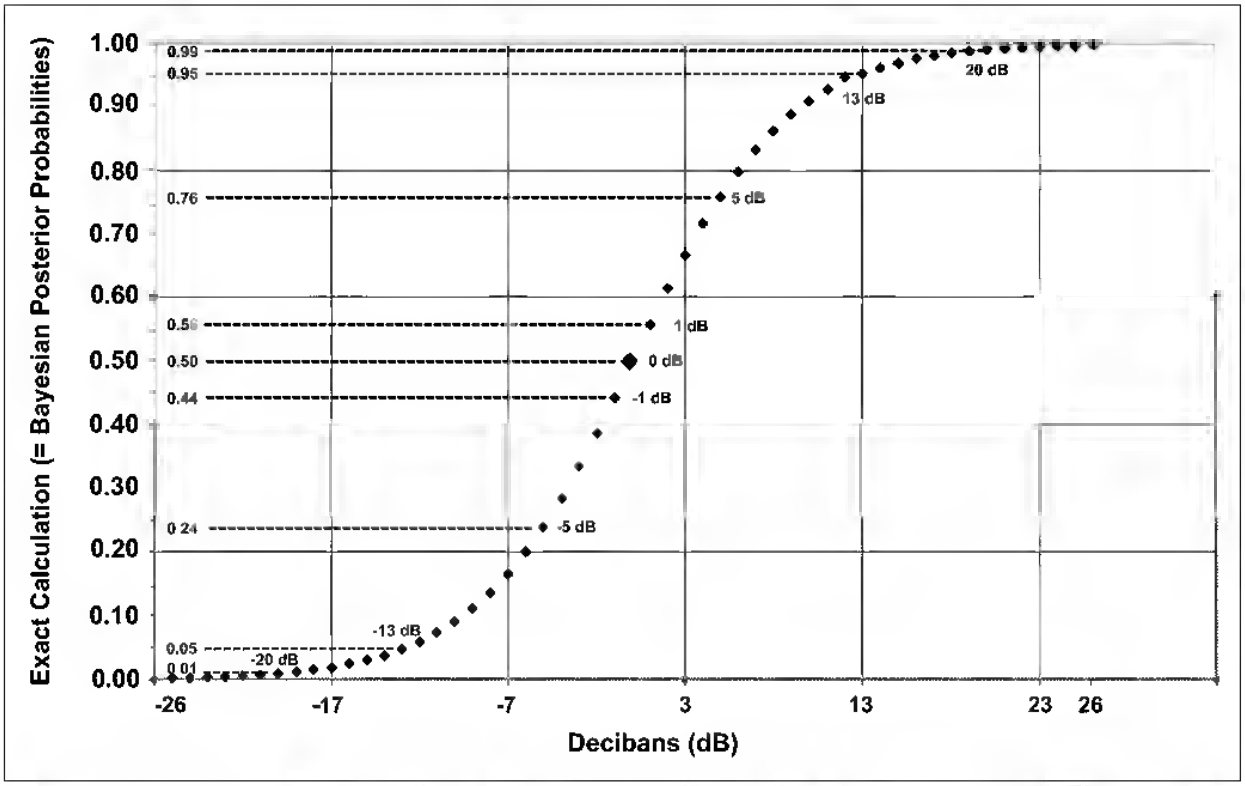

Figure 6. Chart of probabilities showing decibans on the x-axis (logarithmic) and exact probabilities on y-axis. After assigning clues as decibans and adding them, the exact probabilities of this form of sequential Bayes analysis can be read off the y-axis, in the fashion of a slide rule.

Table 1 Decibans (dB) with calculations of probabilities by odds of $10^{n/10}$ 1, which is the fraction $10^{n/10}$ divided by $10^{n/10}$ + 1 Given that decibans are logarithmic, they may be added, e g , 2 dB plus 3 dB = 5 dB Decibans and their exactly equivalent sequential Bayesian probabilities may be read off this table Negative dBs are for contrary hypotheses Zero dB = 0 500 probability Approximate odds ratios are given Important mileposts are bold faced First standard deviation = 3 dB, second S D = 13 dB, third S D = 26 dB

dB	**1**	2	3	4	**5**	6	7	8	9	**10**	11	12	**13**
Prob	**0.557**	0 613	0 666	0 715	**0.759**	0 799	0 833	0 863	0 888	**0.909**	0 926	0 940	**0.952**
Odds	5 4	3 2	2 1	5 2	3 1	4 1	5 1	6 1	8 1	10 1	25 2	15 1	20 1
dB	14	15	16	17	18	19	**20**	21	22	23	24	25	26
Prob	0 961	0 969	0 975	0 980	0 984	0 987	**0.990**	0 992	0 993	0 995	0 996	0 996	0 997
Odds	25 1	30 1	40 1	50 1	60 1	80 1	100 1	125 1	165 1	200 1	250 1	330 1	400 1
dB	**-1**	-2	-3	-4	**-5**	-6	-7	-8	-9	**-10**	-11	-12	**-13**
Prob	**0.442**	0 386	0 333	0 284	**0.240**	0 200	0 166	0 136	0 111	**0.090**	0 073	0 059	**0.047**
Odds	4 5	2 3	1 2	2 5	1 3	1 4	1 5	1 6	1 8	1 10	2 25	1 15	1 20
dB	-14	-15	-16	-17	-18	-19	**-20**	-21	-22	-23	-24	-25	-26
Prob	0 038	0 030	0 024	0 019	0 015	0 012	**0.009**	0 007	0 006	0 005	0 004	0 003	0 002
Odds	25 1	1 30	1 40	1 50	1 60	1 80	1 100	1 125	1 165	1 200	1 250	1 330	1 400

The 95% level of significance does have a good basis. Clues can be "added" as equivalent to numbers of decibans, and the probabilities read off a mental x-axis If at least one taxon of a closed causal group (all members surely of that group) reaches a high probability of being a descendant, all of them are One may note for Figure 5 that 0 95 as the standard scientific minimum of confidence is associated with the beginning of rapid logarithmic rise in probabilities, while 0 99 signals a very tight rise Neither of these two limits to statistical confidence or credibility, the lower for non critical decisions, the higher for critical applications or very complex problems, is really very arbitrary, as is sometimes suggested

THE BAYES FACTOR

Bayes factors (Kruschke 2011 58) have been often used in phylogenetic analysis to determine model selection and species delimitation (Fan et al 2011, Grummer et al 2014, Li & Drummond 2012, Suchard et al 2002, Sullivan & Joyce 2005, Ward 2008) The use of Bayes factors in the present paper is simplified but, as measures of direction of macroevolutionary transformation, Bayes factors are powerful in explaining monophyly

The Bayes factor is a measure of which species best models the ancestral species versus the other species The Bayes factor (B F) is the ratio of the likelihoods of the data for two models It is derived from Harold Jeffrey's (1961) concept of relative betting odds (McGrayne 2011 116) Thus, B F = $Pr(D|M_1)$ / $Pr(D|M_2)$, or, the probability of the data given model 1 divided by the probability of the data given model 2 This is the likelihood ratio (Note This is an odds ratio because a probability would have the both of the different probabilities of both models in the denominator, and the fraction would not rise above 1 0) That is, it measures the change in the odds in favor of the hypothesis when going from the prior to the posterior (Lavine & Schervish 1999) For any *one* hypothesis, if the prior is 0 50, the Bayes factor is simply the posterior probability For *two* hypotheses, if the prior is 0 50, then the ratio of the two posterior probabilities is the Bayes factor (i e , the same as the likelihood ratio) (Kass & Raftery 1995) The Bayes factor is somewhat better than standard hypothesis testing because the latter cannot provide an evaluation of information in

favor of the null, just a way to see if it can be falsified, while Bayes factor analysis can evaluate both the hypothesis and the alternative.

Deciban analysis is the same as sequential Bayes analysis but is simpler. The Bayes factor as used here measures probabilistically the central hypothesis that species 1 is ancestral to all immediate descendants as evaluated by sequential Bayes analysis. This is done directly (with a spreadsheet using the results of one Bayes formula analysis as the prior for another, see online spreadsheets) or more coarsely by using decibans (see Table 1). This is done against the alternative hypothesis that some other species is ancestor (as null). That is, the chance of species 1 generating species 2, 3, ...n, versus the chance of species 2, 3, ...n generating species 1 and the rest.

According to Jeffries (1961), a Bayes factor (odds ratio in favor) for one hypothesis against a null hypothesis may be evaluated thus:

Table 2. Table for interpretng Bayes factors according to Jeffries (1961). Bayes factors in the text leave off the "1" indication but remain ratios

Bayes factor	Value	Probability	Deciban equivalent
1:1– 3:1	trivial	0–0.76	0–5 dB
3:1–10:1	substantial	0.76–0.91	5–10 dB
10:1–100:1	strong	0.91–0.99	10–20 dB
more than 100:1	decisive	more than 0.99	more than 20 dB

Kass and Raftery (1995) also provide significance charts for B.F. expressed to base $\log_{10}$ and $\log_e$, which are scales suitable for certain purposes, but this paper eliminates unnecessary mathematical burdens for the classical systematist readership. To derive a Bayes factor against an alternative hypothesis, the likelihood of the first hypothesis must be divided by that of the second. We first determine the odds ratio for each of the two probabilities, a:b and c:d, which is (a/c)/(b/d) = ad/bc. Here, c and d are commonly the same (i.e., 1). For example, we may have two hypotheses, A of 0.99 or 20 dB, and B of 0.61 or 2 dB. The odds ratio is 100:1/1.5:1, or 67, which may be taken as the Bayes factor. Approximate odds ratios for various positive and negative deciban levels are given in Table 1. Table 2 allows an interpretation of Bayes factors in terms of probabilities and decibans.

GRANGER CAUSALITY AND BAYES FACTORS

Causal connections are determined by predictability as well as correlation. As discussed by Sugiharra et al. (2012), Berkeley (1710, numbered paragraphs 20, 50, 64, and 65) made the observation that simple correlation in time or space is no assurance of a causal connection between one thing and another. This is mainly because there may be a third thing affecting both, and both will change following a causal connection between the third thing and the other two. There may even be a lag time that confounds direct detection of that third causal element. The solution is apparently "Granger causality" (Granger 1969), which promotes predictability rather than correlation for detecting causality. An element is said to "Granger cause" another element if the predictability of that second element declines when the first element is removed from the model, all else being the same (Sugiharra et al. 2012). Information about a causative element must be independent of other elements associated with some particular process-based model.

Predictability is essential in determining monophyly. Speciation may be interpreted as an ecological time series, thus the causal connections of ancestor-descendant relationships may be tested using Granger causality. The assumption used in the present paper is that for any one, two, or more closely related species all with advanced traits, there should be or should have been another with more generalized traits. The null model for the central hypothesis (that species 1—the most

generalized species—is the putative ancestral taxon) is that some other species in the group is the basal ancestor of the group. We can reject the null if species 1 in the group (the causative ancestor), when eliminated, results in very poor predictability of ancestor-descendant relationships among the remaining taxa in the group. Poor predictability would be immediately evident by there being no strong polarization of support towards one of the other species, that is, low Bayes factors. We do not eliminate the putative progenitor completely from the null model, but instead calculate the chance of each of the other species being progenitor of the group. If such a chance is far lower than that of the putative progenitor, and prediction (here actually retrodiction of a serial evolutionary transformation) is much lessened, we can say the "Granger cause" of the ancestor-descendant relationships in the group is species 1, the putative progenitor.

Implied Reliable Confidence Interval (IRCI)

When many models are tested together there may be support between them. IRCI tells you if you have enough data on transformation directions to make any decision at all. Suppose tyou are examining serial species transformation involving one species and a number of other species (1>2, 1>3, 1>4, etc.), and the data on all species transformations support to some extent the same decision that 1>rest. This multiplication of evidence from two or more data sets can be reflected in increased probability that 1>rest. For this the Implied Reliable Credible Interval (IRCI) formula can be used. The IRCI was used by Zander (2006) to evaluate the chance of at least one of several concatenated cladogram branches of moderate credibility support being correct. It uses the fact that there are more than one sources of at least some support. In this case, even 0.10 probability of 1>2 is some support that 1>rest, because if one hypothesis is true, all species transformation directions are true in this closed group.

Unlike Bayes factor analysis, nesting is not necessary since for any set of probabilities of any process, the more processes involved the greater the chance that one is correct. This is a kind of "existence" estimation when probabilities of events are not individually decisive.

For the IRCI formula, because calculating positive support is difficult, calculating negative support and then subtracting from one is easier. The formula is basically 1 minus the multiplied chances that each element is not true ("not true" meaning one minus the probability it is true). This is not the chance of one particular transformation between two species being correct, but the chance that a sufficient number of hypotheses each of less than acceptable probability will support the idea that at least one of them is correct.

If at least one of the models of macroevolutionary transformation is correct (say, 1>2), then the others (1>3, 1>4, etc.) must be because the models are in a closed causal pool. The closed causal pool for Zander's (2006) cladogram analysis was a series of concatenated cladogram internodes, where if one internode is correct then the taxa beyond the series are indeed in a clade of their own. Here the closed causal pool is a set delimited by the decision that they are all related and one of them is a direct or indirect basal ancestral species for all. It does not particularly increase the odds that a particular species is ancestral, but does ensure that the problem is decidable. If the problem is decidable, then the species with the least probable chance of being ancestral are well established as descendants, and the two most likely are the only candidates. If the Bayes factor for those two most likely candidates exceeds 3.1, then the most likely species is well supported as ancestor.

The IRCI is only used when no single Bayesian posterior probability among the results of sequential Bayes' analysis is adequate for a decision. Note that the IRCI deals with probabilities (chance that the hypothesis is correct) not with likelihoods (chance that the data are correct).

Probabilities calculated from different information do not necessarily have to add to 100 percent, but the closed pool ensures they are nested.

Probabilities can be confusing. When used as clues, any probability higher than 0.50 can be added when converted to a deciban. Thus, in sequential Bayes analysis, any probability more than 0.50 (more than zero dB) contributes to total clue decibans, but probabilities less than 0.50 (less than zero dB) reduce the confidence in total clue decibans and therefore in credibility that one species is direct or indirect ancestor of all in the closed causal group.

For IRCI, on the other hand, any probability greater than zero contributes to total confidence that the question of which species is ancestral is decidable. This is because total polarization of clues in the closed causal group contributes to focusing on one or two species as true candidates. Sometimes one species can be singled out to be well supported as ancestral species.

Consider, for example, the contrived situation of species A through E all in one group with A the fairly obvious ancestral species. What is the exact support for A being the ancestral species? Each species has a probability based on various data that it is the direct or indirect ancestral species of the group. An IRCI for the probabilities 0.90, 0.25, 0.20, 0.10, 0.10 for the species A through E series gives 0.95 IRCI, as in IRCI formula (1):

$$(1 - ((1 - 0.90) \times (1 - 0.25) \times (1 - 0.20) \times (1 - 0.10) \times (1 - 0.1))) = 0.95 \qquad (1)$$

and Bayes factor of 3.6 (that is, 0.90 divided by 0.25), which is substantial for species A being the direct ancestral species. This is true even when it does not have the full 0.95 initial probability based on decibans alone. Note, again, that these probabilities do not have to add to 1.00 because somewhat different data is used to calculate each probability.

CONTINUED IN PART 3, THE ANALYSIS

SUPPLEMENTARY MATERIAL

Spreadsheets for calculating Bayes sequential analysis, decibans, and IRCI are available at <http://www mobot org/plantscience/resbot/evsy/sprsh>.

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CLASSICAL DETERMINATION OF MONOPHYLY, EXEMPLIFIED WITH *DIDYMODON* S. LAT. (BRYOPHYTA). PART 3 OF 3, ANALYSIS

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ABSTRACT

The shared ancestral and serial transformative evolutionary relationships of the *Didymodon* s. lat. (Pottiaceae, Bryophyta) group of mosses is investigated. Decibans are used as coarse likelihoods for serial trait transformations in sequential Bayes analysis, here using morphology alone. In convergence analysis, theoretical adaptive radiations and neutral but divergent transformations among the species of the data set are evaluated with estimated deciban support for hypothetical models of serial macroevolutionary change. These are converted to Bayes factors. Direction of macroevolutionary transformation on a caulogram is determined by morphological cladogram position, and maximum Bayes factor (or deciban differential) except when an intermediate taxon may be proposed, either from the extant set or as an unknown shared ancestor that minimizes Bayes factor differences. In cases with model probability near unity, deciban range differences between models are accepted because there was little discrimination with Bayes factors. Estimated monophyly among the segregate genera of *Didymodon* s. lat. is represented by a caulogram of serial macroevolutionary relationships annotated with Bayes factors and deciban differentials for serial species-level transformations.

The moss genus *Didymodon* Hedwig was used (Zander 2013: 80) to demonstrate **superoptimization**, which is the attempted naming of cladogram nodes using novel, advanced trait criteria for determining serial evolutionary transformation direction. The naming of the nodes in that paper was done informally and intuitively in the context of informed expertise, the author having studied the family (Pottiaceae) of *Didymodon* for the past 40 years. Segregate genera were established through cladistic analysis and expert ability to identify **dissilience** (situations of core generative species from which descendants with apparent adaptive or at least novel traits arise). The identification and description of evolutionary process in such dissilient genera is the central means of identifying monophyly for these groups, and this paper sets out what may well be the statistical basis for scientific intuition in classical identification of monophyletic groups.

ANALYSIS OF SEGREGATE GENERA OF *DIDYMODON* THROUGH DECIBAN HEURISTICS

Expert opinion use of decibans is a simple way to use clues in sequential Bayes analysis. Given the assumption that we would like to have a more accurate and reasonable analysis of support than the informal assignment of nearly certain likelihoods as was done by Zander (2013: 80), one can now attempt a formalized heuristic analysis of monophyly in the entire *Didymodon* genus complex consisting of the six segregate genera *Didymodon* s. str., *Exobryum* Zander, *Fuscobryum* Zander, *Geheebia* Schimper, *Trichostomopsis* Cardot, and *Vinealobryum* R.H. Zander. The new method uses sequential Bayes by means of decibans assigned to radiative traits. This formalization is intended to mimic or at least explain the quick apprehension of monophyly of expert scientific intuition. All species weighted for putative ancestral status (i.e., basal species for a monophyletic transformation series) have similar primitive traits for the inclusive s. lat. group. These traits include general and widespread distribution at least relative to the putative descendants, no specialized habitats, moderate size, no specialized or reduced organs, and are sexually reproducing.

Molecular analysis for this group is presently uninformative. A molecular (ITS) analysis of many of the same species of *Didymodon* s. lat. was done by Werner et al. (2005). The results were evolutionarily equivocal as discussed in detail by Zander (2013: 90) because neither heterophyly nor distance on the cladogram beyond that expected from hidden paraphyly or phylogenetic polyphyly were evident.

Does restriction of clues to minimal values degrade analysis? Two different superoptimization analyses are done in each genus' Table, one for assignment of 1 dB (in roman typeface) for each morphological trait, as a benchmark for results from a minimal "clue" to direction of transformation. Then, another assignment is done with variable numbers of decibans (in bold typeface) to reflect estimation of different weights of the clues for each trait (in Italic typeface).

First, any analysis using the present method begins with division of a large group into small working groups of one apparent ancestral species and its evolutionarily derived species, judged by criteria discussed above. Often subgenera and sections indicate such evolutionarily "dissilient" groups. In this case, the infragenera of *Didymodon* s. lat. as promoted to generic status (Zander 2013: 93) were used successfully.

Second, evaluation is done of the chance of species 1 (selected intuitively as ancestral) giving rise to each of the other species as a central hypothesis, assuming groups previously segregated to those with only one extant or postulated generalized ancestral species. The cladogram (Fig. 1) of *Didymodon* s. lat. of Zander (1998, 2013: 80) is used as a preliminary grouping structure for the six segregate genera because it happens to group well the classical subgenera (Fig. 1), which do have only one generalized species. A natural key (e.g., Zander 1993: 82) could just as well be used. These segregates were advanced to genus status by Zander (2013: 93) based on the intuitive assignment of high probability to traits implying directionality of macroevolutionary transformation. Each of these segregate genera is here re-evaluated with sequential Bayes analysis first using a minimal 1 dB for all traits, then second using varying deciban assignments as to probability of macroevolutionary transformation of the specialized species away from each of the most generalized. The deciban assignments are coarse, arbitrarily using only odd numbers, 1, 3, 5 or 7, as approximately as is possible to estimate such assignments. The posterior probabilities associated with multiple decibans can be read off Table 1 in Part 1 of this study.

Third, evaluation is done of the chance of any species n generating species 1 as alternative hypothesis. This is essentially 1 minus the chance that species 1 gave rise to each of the other species. A Bayes factor was calculated from the support values of the central hypothesis and the alternative hypothesis to summarize support for and against the generalized species being the ancestor.

Fourth, when probabilities of descendants that are directly generated by the putative ancestor are each lower than, say, 0.95, the IRCI is figured for the chance that at least one of those species is a descendant. Inasmuch as this is a closed causal group, the fact that one of the direct descendants is reliably a descendant of the ancestral taxon means that they all are. The species with highest probability is then at least tentatively the ancestral species.

Descendants can generate descendants of their own. When there are secondary derivations of two or more species from another descendant species, only those secondarily derived species are used in IRCI calculations. An example is the posterior probabilities of the 1 dB per trait analysis of *Vinealobryum* species. One of the putative descendants, *V. nevadense,* is eliminated as secondarily descended from another descendant. The posterior probabilities of the three putative direct descendants of *V. vineale* are 0.50, 0.61 and 0.61. Combining these through the IRCI formula,

the chance of at least one of the three being a descendant is quite high, 0.93, and thus there is a strong chance they all are. Another example is the 1 dB per trait analysis of *Geheebia* species in which the four apparently direct descendants of the putative ancestral species have posterior probabilities of 0.76, 0.72, 0.67, and 0.76, but an IRCI for these of 0.995, such that one of these taxa are surely a descendant, and thus they all are.

Fifth, with probabilities of two or more models close to unity (100%), Bayes factors are uninformative. Those probabilities near unity, however, are generated by summing evidence in the form of clues. A small difference in probability near unity may provide a low Bayes factor, but may incorporate a major difference in numbers or value of clues. In critical cases, differences in decibans may provide convincing evidence for decisions between hypotheses (models). For instance, in the analysis of *Vinealobryum* (Table 4) with variably assigned dB values, posterior probabilities between the most likely basal generative species 1 (*V. vineale*) and species 2 (*V. brachyphyllum*) are similar for models of each generating direct descendants among the remainder of the species. But adding the decibans for species 1 generating the first tier of descendants, i.e., species 2, 3, and 4, and also for species 2 generating species 1, 3 and 4, the sums of 36 dB and 20 dB reveal nearly twice the evidence or at least significance of the evidence for the first hypothesis, namely 1>immediate descendants (species 2, 3 and 4). The Bayes factor associated with this difference in evidence, however, is only 1.0096.

Clues are external evidence of direction of evolution based on evolutionary theory. In some treatments deciban evidence for the two most likely species (species 1 and 2) is the same, but positive in decibans for species 1 and negative for species 2 (e.g., analysis of *Geheebia* (Table 5). But the values are of different use in that these values do not measure the difference between the two models but between each model and an outside criterion applicable to all the species, a separate model of trait transformation. This is a different use of the same evidential information and the distance in dB as *clues* is thus indeed twice the number of dB involved.

Very high Bayes factors can imply an unknown ancestor. Critical here is the idea that when an ancestral species generates several descendants, any new traits that are shared among such descendants may be considered conservative in that they occur in two or more species or by extension in two or more habitats. This is the case when descendants may be more similar to each other than to the putative ancestor. A shared ancestor may be postulated to encapsulate the conservative traits (see example in *Fuscobryum,* below) and mitigate the high B.F. for such descendants which would otherwise be indicative of membership in a separate genus. So parsimony (as done in cladistics) can be in some cases effective. The traits involved in parsimony must be evaluated first as homologous or evolutionarily connected in some way, however, since traits like isolated distributions and polyploidy (otherwise helpful for determining direction of serial macroevolution) may not be homologously shared.

Conservative traits are easily transmissible. When traits are transmitted from a putative *descendant* to one or more secondary descendants, if such traits are new to the genus, they must then be taken as conservative, that is, they are found in different species and therefore apparently tolerate different selective regimes. If the new traits are multiple, reversals in a *combination* of conservative traits are subject to (low) joint probability of unlinked traits. This must contribute to evaluation of direction of evolution and therefore determination of details of monophyly.

The analyses are presented here in order of numbers of species involved to make understanding the complex analyses easier. Rather than a subset for demonstration purposes, all analyses are given because they each deal with different contingencies:

(1) High B.F. for variable dB assignments but low B.F. for minimal clues (tables 1 and 2).

(2) Postulation of a shared ancestor for descendants more similar to each other than to the progenitor (Table 2).

(3) Derivation of one descendant species from another (tables 3, 4 and 5).

(4) Triple concatenation of descendants supported by no reversals, plus status of a highly derived phenotypically and biotypically diverse descendant with a stenomorphic descendant of its own (Table 5).

Note: Throughout "IDs" means "immediate descendants" of species 1 (i.e., exclusive of secondary speciation of descendant to descendant).

Table 1. Deciban analysis of *Trichostomopsis*. 1 = *Trichostomopsis australasiae*. 2 = *T. umbrosa*. 3 = *T. revoluta*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3
TRAITS	Spec. distrib. human		1, **3**	
	Long whip leaf		1, **5**	
	Bulg. hyal. basal cells		1, **5**	
	Local distr.			1, **3**
	Short leaves			1, **5**
	Unicell. gemmae			1, **7**
	SUM	0, **0**	3, **13**	3, **15**
TOTAL dB DIFF		1	2	3
	>1		-3, **-13**	-3, **-15**
	>2	3, **13**		0, **-2**
	>3	3, **15**	0, **2**	
POST. PROB.		1	2	3
	>1		0.33, **0.05**	0.33, **0.03**
	>2	0.67, **0.95**		0.50, **0.39**
	>3	0.67, **0.97**	0.50, **0.61**	
BAYES FACTORS		1	2	3
	>1		0.50, **0.05**	0.50, **0.03**
	>2	1.99, **19.95**		1.00, **0.63**
	>3	1.99, **31.62**	1.00, **1.59**	
IRCI TOTAL		0.89, **1.00**	0.67, **0.63**	0.67, **0.41**

Table 2. Deciban analysis of *Fuscobryum*. 1 = *Fuscobryum nigrescens*. 2 = Postulated shared ancestor. 3 = *F. perobtusum*. 4 = *F. subandreaeoides*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4
TRAITS	Local distr			1, **3**	1, **3**
	Lvs short		1, **1**	1, **1**	1, **1**
	Apex rounded		1, **3**	1, **3**	1, **3**
	Unicell. gemmae			1, **5**	
	Soroph. lacking			1, **3**	1, **3**
	Leaves dimorphic				1, **7**
	Stems short			1, **5**	
	SUM	0, **0**	2, **4**	6, **20**	5, **17**
TOTAL dB DIFF.		1	2	3	4
	>1		-2, **-4**	-6, **-20**	-5, **-17**
	>2	2, **4**		-4, **-16**	-3, **-13**
	>3	6, **20**	4, **16**		1, **3**
	>4	5, **17**	3, **13**	-1, **-3**	
POST. PROB.		1	2	3	4
	>1		0.37, **0.28**	0.20, **0.01**	0.24, **0.02**
	>2	0.61, **0.72**		0.29, **0.02**	0.33, **0.05**
	>3	0.80, **0.99**	0.72, **0.98**		0.56, **0.67**
	>4	0.76, **0.98**	0.67, **0.95**	0.44, **0.33**	
BAYES FACTORS		1	2	3	4
	>1		0.63, **0.40**	0.25, **0.01**	0.32, **0.02**
	>2	1.58, **2.51**		0.40, **0.03**	0.50, **0.05**
	>3	3.98, **100.00**	2.51, **39.81**		1.26, **2.00**
	>4	3.16, **50.12**	2.00, **19.95**	0.79, **0.50**	
IRCI TOTAL		0.98, **1.00**	0.94, **1.00**	0.68, **0.33**	0.78, **0.67**
IRCI 2>3 & 4			0.94, **1.00**		

Table 3. Decibar analysis of *Didymodon*. 1 = *Didymodon acutus*. 2 = *D. tomadophilus*. 3 = *D. rigidulus* s. str. 4 = *D. ansermocapitatus*. 5 = *D. johansenii*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4	5
TRAITS	Restricted distrib.				1, **3**	1, **3**
	Epixylic					1, **5**
	High elev.		1, **3**		1, **3**	
	Short basal cells		1, **5**			
	Elong. apex		1, **3**			
	Hygric habitat			1, **5**		
	Asex. gemmae			1, **3**		
	Swan neck lf. apex				1, **7**	
	Sporoph. lacking				1, **5**	
	Asex. clavate apical propag.					1, **7**
	Thick, not decid. apex			1, **3**		
	SUM	0, **0**	3, **11**	3, **11**	4, **18**	3, **15**
TOTAL dB DIFF.		1	2	3	4	5
	>1		-3, **-11**	-3, **-11**	-4, **-18**	-3, **-15**
	>2	3, **11**		0, **0**	-1, **-7**	0, **-4**
	>3	3, **11**	0, **11**		-1, **-7**	0, **-4**
	>4	4, **18**	1, **7**	1, **7**		1, **3**
	>5	3, **15**	0, **4**	0, **4**	-1, **-3**	
POST. PROB.		1	2	3	4	5
	>1		0.33, **0.07**	0.33, **0.07**	0.28, **0.02**	0.33, **0.03**
	>2	0.67, **0.93**		0.50, **0.50**	0.44, **0.17**	0.50, **0.28**
	>3	0.67, **0.93**	0.50, **0.50**		0.44, **0.17**	0.50, **0.28**
	>4	0.72, **0.98**	0.56, **0.83**	0.56, **0.83**		0.56, **0.67**
	>5	0.67, **0.97**	0.50, **0.72**	0.50, **0.72**	0.44, **0.33**	
BAYES FACTORS		1	2	3	4	5
	>1		0.50, **0.08**	0.50, **0.08**	0.40, **0.02**	0.50, **0.03**
	>2	2.00, **12.59**		1.00, **1.00**	0.79, **0.20**	1.00, **0.40**
	>3	2.00, **12.59**	1.00, **1.00**		0.79, **0.20**	1.00, **0.40**
	>4	2.51, **63.10**	1.26, **5.01**	1.26, **5.01**		1.26, **2.00**
	>5	2.00, **31.62**	1.00, **2.51**	1.00, **2.51**	0.79, **0.50**	
IRCI TOTAL		0.99, **1.00**	0.93, **0.98**	0.93, **0.98**	0.88, **0.54**	0.93, **0.83**

Table 4. Deciban analysis of *Vinealobryum*. 1 = *Vinealobryum vineale*. 2 = *V. brachyphyllum*. 3 = *V. murrayae*. 4 = *V. nicholsonii*. 5 = *V. nevadensis*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4	5
TRAITS	Restricted distrib.			1, **3**	1, **3**	1, **3**
	Bark	1, **1**		1, **5**		
	Short leaves		1, **3**			1, **3**
	Lf. apex decid.			1, **7**		
	Lf. apex cucul.					1, **7**
	Leaves broad above				1, **5**	
	Laminal cells bistrat.	1, **1**			1, **3**	
	Midrib thick					1, **5**
	Lf. marg. revol.					1, **7**
	Repro. by gemmae		1, **3**			1, **3**
	Sporoph. lacking			1, **5**	1, **5**	1, **5**
	SUM	2, **2**	2, **6**	4, **20**	4, **16**	7, **33**
TOTAL dB DIFF.		1	2	3	4	5
	>1		0, **-4**	-2, **-18**	-2, **-14**	-5, **-31**
	>2	0, **4**		-2, **-14**	-2, **-10**	-5, **-27**
	>3	2, **18**	2, **14**		0, **4**	-3, **-13**
	>4	2, **14**	2, **10**	0, **-4**		-3, **-17**
	>5	5, **31**	5, **27**	3, **13**	3, **17**	
POST. PROB.		1	2	3	4	5
	>1		0.50, **0.28**	0.39, **0.28**	0.39, **0.04**	0.24, **0.00**
	>2	0.50, **0.72**		0.39, **0.04**	0.39, **0.09**	0.24, **0.00**
	>3	0.61, **0.98**	0.61, **0.96**		0.50, **0.72**	0.33, **0.05**
	>4	0.61, **0.96**	0.61, **0.91**	0.50, **0.28**		0.33, **0.02**
	>5	0.76, **1.00**	0.76, **1.00**	0.67, **0.95**	0.67, **0.98**	
BAYES FACTORS		1	2	3	4	5
	>1		1.00, **0.40**	0.63, **0.02**	0.63, **0.04**	0.32, **0.00**
	>2	1.00, **2.51**		0.63, **0.04**	0.63, **0.10**	0.32, **0.00**
	>3	1.58, **63.10**	1.58, **25.12**		1.00, **2.51**	0.50, **0.05**
	>4	1.58, **25.12**	1.58, **10.00**	1.00, **0.40**		0.50, **0.02**
	>5	3.16, **1258.93**	3.16, **501.19**	2.00, **19.95**	2.00, **50.12**	
IRCI TOTAL		0.98, **1.00**	0.98, **1.00**	0.94, **0.97**	0.94, **1.00**	0.74, **0.07**

Table 5. Deciban analysis of *Geheebia*. 1 = *Geheebia fallax*. 2 = *G. ferruginea*. 3 = *G. gigantea*. 4 = *G. maschalogena*. 5 = *G. maxima*. 6 = *G. tophacea*. 7 = *G. leskeoides*. Lightface for 1 dB per trait, bold for variable dB assignments.

SPECIES		1	2	3	4	5	6	7
TRAITS	Moist hab.		1, **3**	1,**3**	1, **3**	1, **3**	1,**3**	1, **3**
	Reddish Lvs. strong rec.		1,**1** 1, **3**	1, **1**		1, **1**		
	Sporoph. rare or lacking		1, **3**	1,**3**				
	Perist. fragile, reduced		1, **1**					
	North distr.			1, **3**		1, **3**		1, **3**
	Pl. very large			1, **3**		1, **3**		
	Lumens angular			1, **7**				
	Lvs. catenul.				1, **5**			
	Asex. gemmae				1, **3**			
	Restr. distr					1, **3**		1, **3**
	Wet limestone						1, **5**	
	Lf. apex rounded						1, **5**	
	Lvs. ligulate						1, **5**	
	Lf. base decur., not winged						1, **3**	
	Costa subperc.						1, **3**	
	Lvs. whip							1, **5**
	Lf. base winged							1, **7**
	SUM	0, **0**	5, **11**	6, **20**	3, **11**	6, **16**	6, **24**	6, **24**
TOTAL dB DIFF.		1	2	3	4	5	6	7
	>1		-5, **-11**	-6, **-20**	-3, **-11**	-6, **-16**	-6, **-24**	-6, **-24**
	>2	5,**11**		-1, **-9**	2, **0**	-1, **-5**	-1, **-13**	-1, **-13**
	>3	6, **20**	1, **9**		3, **9**	0, **4**	0, **-4**	0, **-4**
	>4	3, **11**	-2, **0**	-3, **-9**		-3, **-5**	-3, **-13**	-3, **-13**
	>5	6, **16**	1, **5**	0, **-4**	3, **4**		0, **-8**	0, **-8**
	>6	6, **24**	1, **13**	0, **4**	3, **13**	0, **8**		0, **0**
	>7	6, **24**	1, **13**	0, **4**	3, **20**	0, **8**	0, **0**	
POST. PROB.		1	2	3	4	5	6	7
	>1		0.24, **0.07**	0.20, **0.01**	0.33, **0.07**	0.20, **0.02**	0.20, **0.00**	0.20, **0.00**
	>2	0.76, **0.93**		0.44, **0.11**	0.61, **0.50**	0.44, **0.24**	0.44, **0.05**	0.44, **0.05**
	>3	0.80, **0.99**	0.56, **0.89**		0.67, **0.89**	0.50, **0.72**	0.50, **0.28**	0.50, **0.28**
	>4	0.67, **0.93**	0.39, **0.50**	0.33, **0.11**		0.33, **0.24**	0.33, **0.05**	0.33, **0.05**
	>5	0.80, **0.98**	0.56, **0.76**	0.50, **0.28**	0.67, **0.76**		0.50, **0.14**	0.50, **0.14**
	>6	0.80, **1.00**	056, **0.95**	0.50, **0.72**	0.67, **0.95**	0.50, **0.86**		0.50, **0.50**
	>7	0.80, **1.00**	0.56, **0.95**	0.50, **0.72**	0.67, **0.99**	0.50, **0.86**	0.50, **0.50**	

BAYES FACTORS	1	2	3	4	5	6	7
>1		0 32, **0.08**	0 25, **0.01**	0 50, **0.08**	0 25, **0.03**	0 25, **0.00**	0 25, **0.00**
>2	3 16, **12.59**		0 79, **0.13**	1 58, **1.00**	1 79, **0.32**	0 79, **0.05**	0 79, **0.05**
>3	3 98, **100.00**	1 26, **7.94**		2 00, **7.94**	1 00, **2.51**	1 00, **0.40**	1 00, **0.40**
>4	2 00, **12.59**	0 63, **1.00**	0 50, **0.13**		0 50, **0.32**	0 50, **0.05**	0 50, **0.05**
>5	3 98, **39.81**	1 26, **3.16**	1 00, **1.40**	2 00, **3.16**		1 00, **0.16**	1 00, **0.16**
>6	3 98, **251.19**	1 26, **19.95**	1 00, **2.51**	2 00, **19.95**	1 00, **6.31**		1 00, **1.00**
>7	3 98, **251.19**	1 26, **19.95**	1 00, **2.51**	2 00, **20.75**	1 00, **6.31**	1 00, **1.00**	
IRCI TOTAL	1 00, **1.00**	0 98, **1.00**	0 97, **0.95**	1 00, **1.00**	0 99, **1.00**	0 97, **0.72**	0 97, **0.72**

RESULTS

Monophyly of *Trichostomopsis* (Table 1)

1. *Trichostomopsis australasiae* (Hook. & Grev.) Rob.: assigned ancestral status with no advanced traits, **0 dB** (0.50).
2. *T. umbrosa* (Müll.Hal.) Rob.: specialized distribution in human environments 3 dB; long, whiplike leaf 5 dB; strongly bulging hyaline basal cells 5 dB; **total 13 dB** (1>2 is 0.95).
3. *T. revoluta* (Card.) R.H. Zander: local distribution 3 dB; short-oval to short-elliptic leaves 5 dB; unicellular gemmae 7 dB; **total 15 dB** (1>3 is 0.97).

Conclusion: Monophyly is supported with Bayes factors for 1>2 of 20, and for 1>3 of 31, well supporting *T. australasiae* as ancestral taxon. See Jeffries (1961) assignments of B.F. significances given above in Table 2 of Part 2. After a separate analysis of only 1 dB per trait (minimal clues to direction of macroevolutionary transformation), the B.F.'s are low and IRCI = 0.89, however, there are several other species in the genus that have advanced traits that would increase this measure.

Species 1 and 2 are the two most likely as ancestral for the group. For dB=1, there is a **difference of 9 dB** between 1>IDs (immediate descendants) (6 dB) and 2>IDs (-3 dB), probability of 1>IDs is 0.799, of 2>IDs is 0.333, B.F. of 2.39. For variably assigned dB, the **difference is 39 dB**, probability of 1>IDs (28 dB) is 0.9984, probability of 2>IDs (-11 dB) is 0.0730, B.F. is 14.

Monophyly of *Fuscobryum* (Table 2)

1. *Fuscobryum nigrescens* (Mitt.) R.H. Zander: assigned ancestral status, **0 dB** (0.50).
2. Postulated shared ancestor of *F. perobtusum* and *F. subandreaeoides*: leaves short-ovate 1 dB; apex broadly rounded 3 dB; **total dB 4** (0.72).
3. *F. perobtusum* (Brotherus) R.H. Zander: local distribution 3 dB; leaves short-ovate 1 dB; apex broadly rounded 3 dB; unicellular gemmae 5 dB; sporophytes lacking 3 dB; stems short 5 dB; **total 20 dB** (0.99).
4. *F. subandreaeoides* (Kindberg) R.H. Zander: local distribution 3 db; leaves short-ovate 1 dB; apex broadly rounded 3 dB; leaves dimorphic 7 db; sporophytes lacking 3 dB; **total 17 dB** (0.98).

Conclusion: The deciban assignments for *Fuscobryum perobtusum* and *F. subandreaeoides* are extreme compared to the 0 dB ground of the putative ancestor *F. nigrescens*. When extreme, membership in a different genus is suggested. The two descendants share two traits, and these can be combined in a presently unknown postulated shared ancestor (species 2 in Table 2). This intermediate taxon lowers the polarization considerably, but if (1) it can be found in nature in the future and has no intermediate other traits, or (2) examination of other species emphasizes clustering of two apparent descendant species, then the causal pool is broken and taxonomic distinction of two

genera is advised. Monophyly of *F. nigrescens* > unknown shared species is supported with a Bayes factor of 2.51, a minor signal that is tolerable because it allows one to reject 1>3 at 100 and 1>4 at 50 and instead countenance 2>3 at 40 and 2>4 at 20. At 1 dB per trait, B.F.'s are minor but for 1>2 and 3 the IRCI = 0.98, while for 2>3 and 4, the IRCI is 0.94, which is just barely acceptable.

Species 1 and 2 are most likely. For dB=1, there is a **difference of 4 dB** between 1>IDs (2 dB) and 2>IDs (-2 dB), probability of 1>IDs is 0.613, of 2>IDs is 0.387, B.F. of 1.58. For variably assigned dB, the **difference is 8 dB**, probability of 1>IDs (4 dB) is 0.720, probability of 2>IDs (-4 dB) is 0.284, B.F. is 2.54, like the IRCI, just barely acceptable.

Monophyly of *Didymodon* s. str. (Table 3)
One might note here that *Didymodon rigidulus* s. lat. in the cladogram of Zander (2013: 80) is presently comprised of *D. acutus* and *D. icmadophilus*.

1. *Didymodon acutus* (Bridel) K. Saito: no advanced traits, **0 dB** (0.50).
2. *D. icmadophilus* (Müll.Hal.) K. Saito: higher elevation habitats 3 dB; short basal cells 5 dB; elongate leaf apex 3 dB; **total 11 dB** (0.93).
3. *D. rigidulus* Hedw.: hygric habitat 5 dB; asexual reproduction by gemmae 3 dB; thickened but not deciduous leaf apex 3 dB; **total 11 dB** (0.91).
4. *D. anserinocapitatus* (X.-j. Li) R.H. Zander: restricted distribution 3 dB; higher elevation habitats 3 dB; unique asexual reproduction by deciduous swan-necked thickened leaf apex 7 dB; sporophytes lacking 5 dB, **total 18 dB** (0.98).
5. *D. johansenii* (Williams) Crum: restricted distribution 3 dB; epixylic substrate 5 dB; asexual reproduction by clavate or cylindric but not swan-necked apical leaf propagulum 7 dB; **total 15 dB** (0.97).

Conclusion: Although the deciban polarization is strong when variably assigned, these species are all clearly related and the differences from the putative progenitor, *Didymodon acutus,* are clearly specializations. Monophyly is well established with Bayes factors for 1>2 of 13, 1>3 of 13, 1>4 of 63, and 1>5 of 32 for *D. acutus* as ancestral taxon. The IRCI figures are high for most transformations but are superfluous because of the high probabilities. If each trait were assigned 1 dB, then B.F.'s are low, but IRCI = 0.99 for 1>rest. For 1 dB assignments, however, IRCI values for certain other species being progenitors are also high, and assigning minimal clue values is not valid for this genus. The decision to derive *D. anserinocapitatus* from *D. icmadophilus* in the caulogram (Fig. 2) is based on a Gestalt evaluation of similarity of habitats and areolation of the excurrent costa.

Species 1 and 2 are most likely. For dB=1, there is a **difference of 12 dB** between 1>IDs (9 dB) and 2>IDs (-3 dB), probability of 1>IDs is 0.888, of 2>IDs is 0.333, B.F. of 2.67. For variably assigned dB, the **difference is 44 dB**, probability of 1>IDs (37 dB) is 0.9998, probability of 2>IDs (-7 dB) is 0.1660, B.F. is 6.02, which is quite acceptable.

Monophyly of *Vinealobryum* (Table 4)
1. *Vinealobryum vineale* (Brid.) R.H. Zander: taken as nearly primitive, some biotypes with two traits shared by some advanced species and assigned a minimal 1 dB each; **total 2 dB**.
2. *V. brachyphyllum* (Sull.) R.H. Zander: short leaves 3 dB; reproduction by gemmae 3 dB; **total 6 dB** (0.80).
3. *V. murrayae* (Otnyukova) R.H. Zander: bark habitat 5 dB; restricted distribution 3 dB; sporophytes lacking 5 dB; odd asexual reproduction 7 db; **total 20 dB** (0.99).
4. *V. nicholsonii* (Culm.) Zander: restricted habitat 3 dB; sporophytes lacking 5 dB; leaves broadened above 5 dB; laminal cells bistratose 3 dB; **total 16 dB** (0.98).

5. *V. nevadense* (R.H. Zander in R.H. Zander, L.R. Stark & Marrs-Smith) R.H. Zander: restricted distribution 3 dB; sporophytes lacking 5 dB; leaves short 3 dB; leaf apex cucullate 7 db; leaf midrib thickened 5 dB; leaf margins loosely revolute 7 dB; asexual reproduction by gemmae 3 dB; **total 33 dB** (0.9995). The reliability of direct transformation with *V. vinealе* as basal to the serial clade is apparently near certain (i.e., *V. nevadense* is clearly in this genus), but species 5 is doubtless a descendant of species 2 (highly specialized morphology and habitat, found on margins of range of species 2), from which it differs without trait reversals. Species 2 may be taken as serially intermediate between species 1 and 5.

Conclusion: Sequential Bayes analysis indicates monophyly with *V. vinealе* or *V. brachyphyllum* as ancestral taxon of the monophyletic group less species 5 is near certain, with B.F. for 1>3 of 63, and for 1>4 of 25, and for 2>3 of 25 and 2>4 of 10. Given that *V. brachyphyllum* seems specialized for human dispersal, has less biotypic variability, and given that *V. brachyphyllum* shared two advanced traits with *V. nevadense,* then postulating *V. brachyphyllum* as basal progenitor of the genus would require more dB reversals for 2>1 than for 1>2. *Vinealobryum vinealе* is the better choice for basal progenitor. If the same were calculated at only 1 dB per trait, IRCI = 0.967. Following the cladogram, acknowledging similarity of the two taxa and contiguity of ranges, and the lack of reversals needed for 2>5, the highly derived *V. nevadense* is considered a descendant of the not-very-advanced species *V. brachyphyllum* by 27 db (0.998+). The IRCI calculation is of no help with this analysis.

Species 1 and 2 are most likely. For dB=1, there is **no difference of dB** between 1>IDs (4 dB) and 2>IDs (4 dB), probability of 1>IDs is 0.714, of 2>IDs is 0.714, B.F. of 1.00. For variably assigned dB, the **difference is 16 dB**, probability of 1>IDs (36 dB) is 0.9997, probability of 2>IDs (20 dB) is 0.9901, B.F. is 1.0098. For variably assigned dB, there is nearly twice the evidence in favor of 1>IDs than 2>IDs, though B.F. is negligible.

The ancestral taxon of the genus *Vinealobryum,* which is basal toof the whole *Didymodon* s. lat. complex, is presently unclear. Several morphologically complex species in various genera with red KOH reactions are candidates, including *Erythrophyllopsis andina* (Sull.) R.H. Zander, *Mironia stenotheca* (Thér.) R.H. Zander, or perhaps some species of *Bryoerythrophyllum* Chen.

Monophyly of *Geheebia* (Table 5)

1. *Geheebia fallax* (Hedw.) R.H. Zander: assigned ancestral status with no advanced traits, **0 dB** (0.50).
2. *G. ferruginea* (Bescherelle) R.H. Zander: moist habitats 3 dB; plants reddish 1 dB; leaves strongly recurved 3 dB; sporophytes rare 1 dB; peristome fragile, often absent 1 dB; **total 11 dB** (0.89).
3. *G. gigantea* (Funck) Boulay: moist habitats 3 dB; northern distribution 1 dB; plants reddish 1 dB; plants very large 3 dB; laminal cells lumens angular, trigonous 7 bB; **total 20 dB** (0.94).
4. *G. maschalogena* (Renauld & Cardot) R.H. Zander: wet habitat 1 db; leaves catenulate-incurved when dry 5 db; asexual reproduction by gemmae 3 dB; **total 11 dB** (0.89).
5. *Geheebia maxima* (Syed & Crundw.) R.H. Zander: northern areas 3 dB; moist habitats 3 dB; restricted distribution 3 dB; stems and leaves enlarged 3 dB; sporophytes lacking 3 db; **total 16 dB** (0.91).
6. *G. tophacea* (Brid.) R.H. Zander: wet limestone habitat 5 dB; leaf apex often blunt or rounded 5 dB; leaf base often with broad decurrencies but scarcely winged 3 dB; costa often ending before leaf apex 3 dB; peristome reduced 5 dB; **total 24 dB** (0.99).
7. *G. leskeoides* (K. Saito) R.H. Zander: northern areas 3 dB; spray zones, wet areas 3 dB; restricted distribution 3 dB; leaves with whiplike apex 5 dB; leaf base winged 7 dB; sporophytes lacking 3 dB; **total 24 dB** (0.98).

Conclusion: Monophyly of *Geheebia fallax* as basal progenitor is strongly supported with B.F. for 1>all species being higher than 10. *Geheebia maxima* is considered derived from *G. ferrugmea* (Fig. 2) as a large, somewhat derived form characteristic of hyperoceanic climates, while *G. gigantea* is apparently an extreme endpoint of the same serial transformation, being even larger than *G. maxima* while *G. maxima* has occasional weak differentiation of the trigonous areolation typical of *G. gigantea*. This triple macroevolutionary transformation series has no reversals. Note here that a B.F. of 1 (as in *G. ferrugmea* > *G. maxima*) or indeed any low B.F. is not a negative result, a B.F. of 1 corresponds to a posterior probability of 0.50 for the transformational direction.

Species 1 and 2 are most likely. For dB=1, there is a **difference of 20 dB** between 1>IDs (14 dB) and 2>IDs (-6 dB), probability of 1>IDs is 0.9610, of 2>IDs is 0.2400, B.F. of 4. For variably assigned dB, the **difference is 44 dB**, probability of 1>IDs (46 dB) is 0.999975, probability of 2>IDs (2 dB) is 0.6131, B.F. is 1.63.

Geheebia leskeoides is considered (Fig. 2) derived from *G. tophacea* in spite of the strong deciban polarization of *G. tophacea* because the latter is biotypically rich as well as phenotypically variable, and there are collections that lack many of the derived features of the species. Perhaps it would have been better to select one "most ancestral" of the biotypes of *G. tophacea* for this analysis. The strongly and broadly decurrent leaf margins are shared by both species and exaggerated in *G. leskeoides*. Although Table 5 shows a high B.F. for *G. ferruginea* > both *G. tophacea* and *G. leskeoides*, these last two are considered a different taxonomic set and possibly of an unrecognized genus (distinguished mainly by distinct, broadly decurrent leaf margins or auricles) and the apparent B.F. polarization simply reflects strong differences at a higher taxonomic level. Likewise, the B.F. of 100 for *G. fallax* > *G. gigantea* reflects the high differentiation of the latter species and serves only to emphasize that fact that if *G. gigantea* is a member of the closed causal group, then *G. fallax* is basal to that group if perhaps not the immediate ancestor of all species.

Monophyly of E*xobryum*

Exobryum asperifolium (Mitt.) R.H. Zander is presently the only species in the genus *Exobryum*, yet it has derived traits (for this group of genera) of restricted habitat, brick-red coloration, stem central strand usually absent, and peristome short, erect. Further study may turn up ancestral or quasi-ancestral species in this genus. Until then one must assume that an unknown shared ancestor probably of the genus *Exobryum* connects *E. asperifolium* and *Vinealobryum* or *Geheebia* (see Figs. 1 and 2).

Discussion

Superoptimization confirms the initial cladogram. The intent of formalization is to avoid or preclude psychological bias in heuristics; to demonstrate the utility in interpreting data following established evolutionary theory of classical methods over axiomatic, hyperprecise solely numerical methods; and, discover fundamental aspects of physics and statistics imbued in human scientific pursuits. A re-analysis was done for all segregate genera in the cladogram of Zander (2013) of the genus *Didymodon* s. lat. with individual traits assigned particular deciban measures for probability of transformation from a putative ancestral taxon. This formalization confirmed the general form of the morphological cladogram (Zander 2013) that used the initial intuitive assignment of near certainty to the advanced traits, but details here modified somewhat. That cladogram also was here capable of being compressed into an easily comprehended format, and fits aspects of both cladistic and classical forms of analysis, relying on established evolutionary theory as informative of direction of evolutionary transformation.

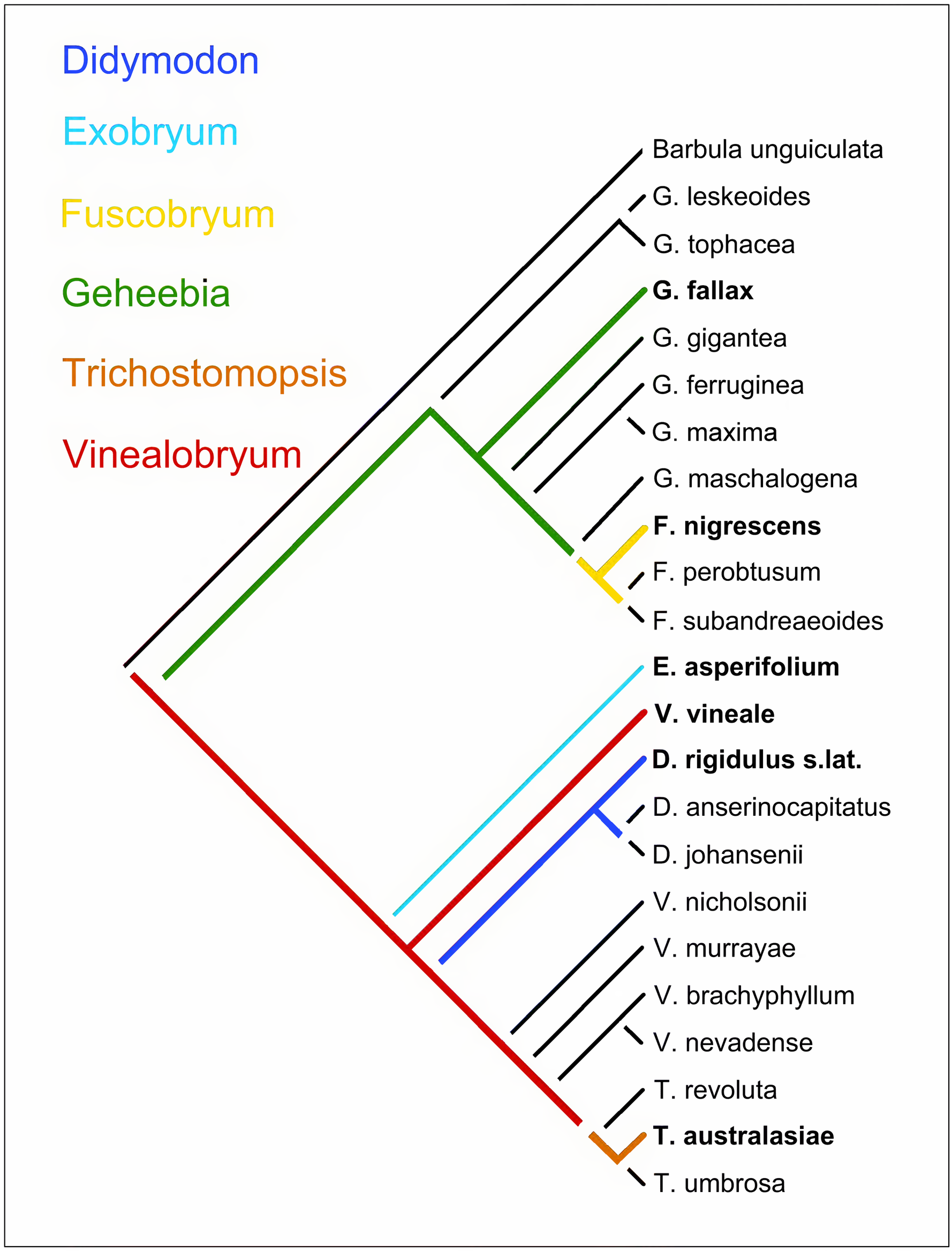

Figure 1. Morphological cladogram of genera in the *Didymodon* s. lat. group, modified from Zander (2013: 80). This demonstration includes only a few of the species known for each genus. Bold colored lines are postulated as deep ancestors of the same name as the generalized species (in bold on the right) and narrower black lines as putative descendants of the generalized species. Decisions for progenitor and descendant status were given intuitively by Zander (2013); formalization of these decisions is given in the tables and summarized in Figure 2.

A caulogram shows both shared ancestral taxa and serial transformations. The caulogram of Figure 2 summarizes the serial macroevolutionary relationships of the *Didymodon* s. lat.

complex estimated from data and theory. Given that software for automatically drawing caulograms does not yet exist, a graphics program must be used. Any software that can make ellipses (see Part 1, Fig. 1) that can be made to touch is acceptable. Or a commagram version (e.g. Fig. 2 of this Part) can be devised by making a circle, erasing a portion, and adding two curving vees. The present author uses NeoPaint (NeoSoft 2012), which is inexpensive but flexible.

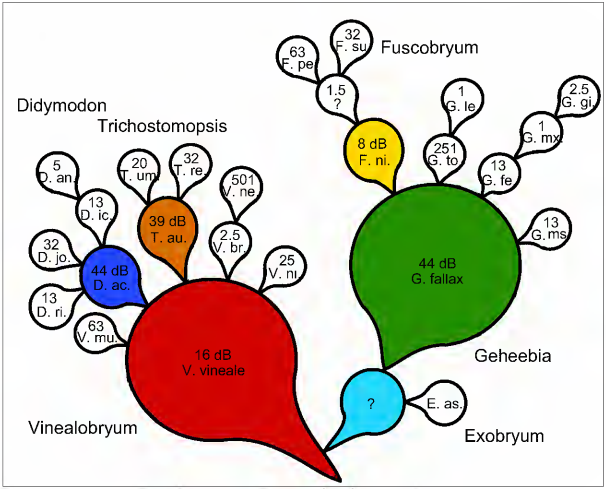

Figure 2 Caulogram showing serial macroevolutionary relationships of the *Didymodon* s lat complex obtained from morphological cladistics and deciban analysis. Some species epithets are uniquely identified by two letters. Bayes factors supporting direction of macroevolutionary transformation in closed causal groups are given for descendant species based on variable deciban assignments per trait. Deciban differences between models of the two most likely progenitors (species 1 > immediate descendants and 2 > immediate descendants) are given for best putative progenitor. Question marks denote postulated, presently unknown shared ancestral taxa. The macroevolutionary formula (boldface for inferred ancestor) for this caulogram is **vinealis** > mu, ni, (**ac** > jo, ri, (**ic** > an)), (**au** > um, re), (**br** > ne), (**?** > as, (**fallax** > ms, (**to** > le), (**fe** > **mx** > gi), (**ni** > (**?** > pe, su))) Colors denote inferred central ancestral taxa, including the unknown shared ancestor of *Exobryum asperifolium* and *Geheebia fallax,* which is probably a generalist species in the genus *Exobryum*.

In Figure 2, Bayes factors are given for each species that is apparently derived from a progenitor, known or unknown, based on transformations of what are taken to be mostly adaptive traits. Deciban differences between models of the two most likely putative progenitors generating the immediate descendants (i.e., exclusive of descendants derived from descendants) are given for the one species most favored as putative progenitor. The probabilities upon which Figure 2 is based are dealt with as clues of various importance, and are frequency estimates only in the sense of informal

expert apprehension of variability during past taxonomic study. Species that are basal and generalist are arranged following cladistic (shared ancestry) relationships using apparently conservative traits. Ability to identify serial relationships and to specify Bayes factors or deciban differences for macroevolutionary transformations is a statistical basis for monophyly. Basing direction of transformation of traits mainly on theoretical adaptive radiations or neutral but unique traits is here substituted for the dubious practice of phylogenetic mapping of trait changes on molecular trees.

No trait reversals is an ideal. The high level of credibility for some polarizations can be overkill for purposes of making a classification, but may be correct given Dollo evaluation of irreversibility of evolution of whole taxa. Both Gould (1970) and Simpson (1953: 311) have pointed out that the chances of the whole genetic system reverting to a complete ancestral state set (as in macroevolutionary reversal to a primitive state set) are infinitesimal. The preferment of no trait reversals in estimating macroevolutionary transformations in the present analysis is important, but may be disregarded in cases of biotypic complexity of the ancestral species (see case of *Geheebia tophacea* above), when no reversals may be expected between a *particular* biotype of primitive traits and a postulated stenomorphic descendant.

Using second-best models is often intuitively clearly wrong. We can say that the chance of one descendant generating another descendant is commonly very small when descendants are more similar to the putative progenitor than to each other. The exception is for situations in which transformation of one descendant into another involves no reversals or for which the reversals are trivial. Radiative adaptation from a generalist ancestor involves or should involve no reversals excepting traits that appear more basal on a standard morphological cladogram than those of the generalist ancestor, and these are commonly few or if many then indicative of higher taxonomic distinction. For example, a putative ancestral-descendant relationship that involves a fully generalized ancestor is supported by positive traits estimated by decibans, and also supported by requirement of no reversal in any advanced traits. But for estimation of the probability of an advanced species actually being ancestor to both the putative ancestor and all the other advanced species, separate reversals from advanced to primitive status are required and very low joint probability comes into play.

At minimum probability levels (i.e., the minimal "clue"), the support via reversal requirement for transformation in the opposite direction is 0.443 probability (i.e., minus one deciban) to the power of the number of (independent) traits requiring reversal. Reversal of four independent (neutral, non-adaptive, or otherwise unlinked) advanced traits at the lowest detectable level of assignable probability (0.433) for each 0.433^4, or 0.035, which translates to a tiny credible interval. But even with a minimal assignment of 0.433 for a set of reversals of a group of linked traits (e.g., all required for adaptation to hygric habitats) when a group of several species involves additional reversals, the additional joint improbability of full and complete reversal of advanced traits in the group if the putative generalized ancestor were *not* the ancestor is decisive. This leads to high Bayes factors comparing odds of a generalized species being basal to the monophyletic group versus that of one of the more advanced species being ancestral, particularly the most advanced species.

There are good heuristics in classical systematics. An appropriate heuristic is when putative descendants are more like the ancestor than each other then they derive directly from that ancestor. Secondary derivation of descendant to descendant is indicated by a no reversal of traits from one descendant to another, e.g., of *V. brachyphyllum* to *V. nevadense*, or of *G. fallax* to *G. ferruginea* to *G. maxima* to *G gigantea*. From the Bayes factor matrices (tables 1 to 5), quite clearly the immediate descendants in general are usually more similar to the immediate progenitor than to each other, except in the cases of apparently secondary speciation either from each other or from a postulated unknown shared ancestral species.

At least in the present case, most nodes can be assigned to known taxa. The object of superoptimization is to parsimoniously determine the minimum of shared ancestors, known or merely inferred, that explain both synapomorphies and autapomorphies. That number of shared ancestors for the *Didymodon* complex of segregate genera is 10 known species, and 2 unknown species (Fig. 2).

Conclusions

What then is the statistical basis for the heuristic used in classical systematics to estimate monophyly? The Turing decibans are defined as $10^{n/10}$:1. Because they are logarithmic, they can be added. One can easily miss the significance of this when explaining that computers were mere adding machines back in the 1940's. In fact, adding logarithms mentally may be the exact way we use clues every day to make decisions. Things "add up." One clue plus one clue equals two clues logarithmically, five clues plus eight clues equals something more than just 13 clues or probabilistic equivalent of 13 clues, which is a 0.95 probability, the minimum for scientific decisions.

There are 12 inferred ancestral species (Fig. 3) in this study, with 198 total decibans supporting inferred serial macroevolutionary relationships, or 16 dB per taxon transformation. This translates to 0.975 probability or an average of 40:1 in favor of each hypothesis of transformation. This is good evidence that the study was successful.

The details of adding clues involve adding logarithms as with a slide rule. The rapid increase in significance when dealing with clues requires, however, an innate logarithmic scale. Do we have such? Classical systematists certainly do not formally or informally compute $10^{n/10}$:1, or use the complex formula for sequential Bayes analysis. Yet common processes in nature must be described in logarithmic terms. A logarithmic curve is also responsible for a particular sensibility about the use of 0.95 as a basic minimal confidence or credible level for noncritical scientific study, and 0.99 for critical studies. I suggest that deciban-based clues in the context of a mental "slide rule" similar to the logarithmic arrangement of deciban probabilities in Figure 6 of Part 2 of this study may be the way we estimate the serial evolutionary transformation associated with monophyly.

If the average clue is of 5 or 7 decibans, that is, good but not good enough to be convincing about direction of evolution, then this would explain why one character alone is often considered insufficient in classical taxonomy to characterize a new species (13 dB provide 0.95 assurance). This may not be quite as circular as it seems, because it suggests that the perceived value of traits carrying information about direction of serial evolutionary transformation are the unacknowledged criteria for perceived level of species delimitation.

Parallel traits presage conservative tendencies. The cladogram results are accepted here as a quick way of determining direction of evolution of traits that are at least "locally" non-adaptive. This is because a fault of morphological cladograms is used to advantage. A cladogram with genera and species will have species separately derived from the same ancestor randomly associated as sister groups because of parallel traits misinterpreted as those from an unknown shared ancestor. Those "synapomorphic" parallel traits are signals of conservative tendencies presaging evolution of a new genus from the old, and genera distal to such nodes are evolutionarily trailed by one or more nodes in the ancestral genus of ancestral traits implying a transformative relationship at the genus level.

Given uncertainties ignored in phylogenetic analyses, evolutionary caulograms may not be as precise or apparently highly supported as phylogenetic studies. In the case of *Didymodon* s. lat., the segregate genera *Fuscobryum* and *Trichostomopsis* are based on unnamed nodes quite distant from the outgroup in the original cladogram (Fig. 1), an outgroup sufficiently like the above candidates to be acceptable. *Didymodon* is to some extent embedded in *Vinealobryum,* and

Exobryum earns an indeterminate position near the base of the cladogram. The caulogram reflects this. It is possible that analysis of reduction of primitive traits and elaboration by evolutionarily local unique traits through deciban analysis will provide a caulistic substitute, check, or complement to morphological cladistic analysis at the level of higher taxonomic categories, but for the nonce the cladogram of Figure 1 suffices for position of genera in the caulogram.

This paper supports the assertion of Zander (2013: 31) that mathematics, physics, and statistics form the process-based backbone of causal induction of evolutionary relationships involved in classical systematics. This is through formalization of informed, intuitive, Gestalt, or omnispection methods, revealing a fundamental rationale for evolution-oriented taxonomic decisions based on expertise and long familiarity with morphological and ecological variance in groups. Note that advanced traits in *Fuscobryum* were used above to postulate an unknown shared ancestral species intermediate between a putative ancestral generalist taxon and the descendants as a prediction of some future discovery or a retrodiction of an extinct taxon. In this case, the descendants *did not* resemble the ancestor more than they did each other.

Prediction from caulograms means that one expects new or recently studied taxa to either fit into a known serial macroevolutionary transform or to be a generalist ancestor of one or more rather specialized descendants. Cladistics does not and cannot predict in this manner (i.e., what to search for in nature and a process-based explanation for placement in an evolutionary classification). After 250 years of Linnaean taxonomy and 150 years of Darwinian theory in systematics, classical clue-based classification remains highly predictive because well established in both evolutionary and statistical theory.

How we do it. The deciban method of determining monophyly uses both data sets of shared traits (preliminary cladogram) and those of unique or adaptive traits (superoptimization of the cladogram). It is capable of distinguishing serial macroevolutionary changes (rather than branch order excepting parallelism) and can provide a probabilistic basis for evaluation of such changes. The ultimate result is a caulogram (Besseyan cactus) with a Bayes factor assigned to each descendant, or a deciban differential for the first two most likely species when Bayes factors are inconclusive. It is probable that this statistical structure is the long-hidden basis for classical evolutionary systematics.

The future. According to Marois and Ivanoff (2005), the human brain has a hundred billion neurons and several hundred trillion synaptic connections. Humans can decode complex images in 100 milliseconds and store as much as 10^9 bits of information over a lifetime. We are limited by being able to attend to and perform little more than one task at a time. This is due to bottlenecks in information flow, including about 0.5 second for consolidating a stimulus in visual short-term memory, severe limitation in information stored in visual short-term memory, and several hundred milliseconds to select a response. Thus, although our ability to act on information is slow, the flexibility and power of each decision can be immense. This paper gives reasons why computerized analytics based solely on shared ancestry can be misleading, even though fast, precise, and duplicable with different data. A return to human-mediated, thoughtful analysis using classical and certain phylogenetic techniques is not only recommended but is promoted as essential to ensure the effectiveness of evolutionary, biodiversity, and conservation studies.

This paper uses the deciban as minimum clue, about the same as the "just noticeable difference" of a 1–2 percent increase in stimulus intensity in the psychophysics of E.H. Weber (Gregory 1987: 405). Psychophysics is an attempt to formalize and quantify judgment (Poulton 1987: 667). Category rating uses a small range of particular magnitudes that makes judgments easier, such as the 1, 3, 5, and 7 deciban levels used in the present paper. Such ratings provide a logarithmic relationship between stimulus and response:

$$R = K + n \log S \quad (1)$$

where R is the subjective response, S is the stimulus, and K and n are constants.

Information theory (Shannon & Weaver 1963) is presently a well-developed theoretical foundation for cybernetics and data interpretation. Of some relevance to systematic analysis is the fact that data in terms of decibans can be directly converted to data in terms of bits. Decibans and bits both are logarithmic. One ban (10 decibans) corresponds to about 3.32 bits, i.e., logarithm of 2 to the base 10, and a deciban is about 0.33 bits. A 0.99 probability (20 decibans) is about equal to 6.5 bits, while 24 dB yields 0.9962 probability, or 1 byte of 8 bits. Also, 1 standard deviation is 3 dB (or 1 bit), 2 s.d. are 13 dB (or 4.25 bits), and 3 s.d. are 26 dB (or 8.6 bits). Thus, a byte is an unequivocal unit of information (it may be wrong information, but it is decidedly information).

As explained for the non-mathematician by Gleick (2011: 228), the probability of a particular coded message should be a weighted sum of the probabilities of the individual symbols. Log to base 2 (or $\log_2$) is most often used. When the probabilities are equal:

$$H = n \log_2 s \quad (2)$$

where H is the measure of information (or entropy), n is a constant, and s is the number of possible symbols. Note the similarity with the stimulus-response formula (1). Although Shannon entropy equates to uncertainty, this non-intuitive definition can be addressed by interpreting H as how much uncertainty is discarded when the message is decoded. The more uncertainty, then, the better. This is similar to K. Popper's bold hypothesis, which is more meaningful than hypotheses that tell one little when demonstrated correct. When the probabilities of each symbol are different, then:

$$H = -\sum p_i \log_2 p_i \quad (3)$$

that is, information in bits is measured by summing the probabilities of each symbol, p_i, just as decibans are summed in the present paper.

Given similarity of use, equivalencies and dissimilarities of decibans and bits are important. One deciban is the minimum information detectable as a clue, or 0.557 probability. One bit (3 dB) is the minimum information needed to make a decision between two alternatives. That decision is 3 decibans, or 0.666 probability, conveniently 1 standard deviation. A decision at 0.666 probability is only valid in the case of betting on several events, each at 0.666, in which you will come out ahead 2/3 of the time. It is not valid for scientific decisions on which further study is to be based. That high level is 0.95 probability (at least for non-critical decisions), which is 13 decibans or 4.3 bits. This is a little more than half a byte (8 bits), and is the boundary for 2 standard deviations. A byte of information is 24 dB, while 26 dB is 0.997, or 3 standard deviations. This last level of confidence is that for confirmed studies with 0.95 probability.

Given that information theory is highly developed, addressing such subjects as joint entropy, conditional entropy, mutual information, information divergence, source theory, information rate, and other complex techniques for dealing with data, future analysis in systematics (in addition to, say, the Akaike information criterion used in phylogenetics) might well make more use of already well-founded information theory.

SUPPLEMENTARY MATERIAL

Spreadsheets detailing analysis for Tables1–5, calculating Bayes sequential analysis, decibans, and IRCI are available at <http //www.mobot.org/plantscience/resbot/evsy/sprsh>.

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LITERATURE CITED

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UPDATED CLASSIFICATION AND HYPOTHETICAL PHYLOGENY OF *ERYTHRANTHE* SECT. *SIMIOLA* (PHRYMACEAE)

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ABSTRACT

Revised versions of the informal classification and phylogenetic diagram of the 50 species of *Erythranthe* sect. *Simiola* are presented, with comments on rationale for the arrangements. Three main lineages are recognized: the Madrensis group (x = 8), the Glabrata group (x = 15), and the Guttata group (x = 7). Within the Guttata group, species of the Nudata and Tilingii subgroups apparently do not intergrade with others. *Erythranthe glaucescens*, *E. corallina*, *E. unimaculata*, and perhaps *E. cupriphilus* also appear to be morphologically isolated, as are *E. brevinasuta* and *E. lagunensis*, which occur in Baja California and Baja California Sur apart from others of sect. *Simiola*.

An infrasectional classification of the 50 species of *Erythranthe* sect. *Simiola* is outlined here. The current version is modified from the original presented in a taxonomic revision of sect. *Simiola* (Nesom 2012). An associated phylogenetic diagram (Fig. 1) is modified from an earlier one shown as part of a commentary (Nesom 2013) noting that assumptions regarding patterns of relationships within sect. *Simiola* should be considered in context of the whole group of species.

The arrangement of species in the classification is based primarily on morphological similarities, geography, and chromosome number. The phylogenetic diagram provides a visualization of the classification and incorporates a few elements regarding evolutionary polarity. The phylogenetic hypothesis is largely subjective and highly unresolved but at least provides a starting point, extending the analysis of Beardsley et al. (2004), for more detailed study.

The phylogenetic study by Beardsley et al. (2004) included 11 species of *Erythranthe* sect. *Simiola* (identities not confirmed, see comments in Nesom 2012). The closest relatives of sect. *Simiola* are indicated to be sect. *Exigua* (comprising the single species *E. exigua*) and the sister pair sect. *Mimulosma* (20 species; base chromosome number x = 8) and sect. *Mimulasia* (11 species; base chromosome number x = 8). x = 8 also is the base for other *Erythranthe* sections for which a chromosome number is known (i.e., sects. *Erythranthe*, *Monimanthe*, *Paradantha*, and *Simigemma*), except for x = 9 in sect. *Monantha* (comprising *E. primuloides* and *E. linearifolia*). Thus x = 8 is assumed to be the primitive number for sect. *Simiola*. It also is the base number for all the Phrymaceae, according to analysis by Beardsley et al. The position of the x = 7 lineage of sect. *Simiola* as derivative compared to the Madrensis and Glabrata groups is reflected in the Beardsley et al. analysis.

Broad features of the classification/phylogeny and related observations

1. The Madrensis group (x = 8) and Glabrata group (x = 15) are positioned as coordinate to the rest of sect. *Simiola* because of their distinction in chromosome number and geography. A base chromosome number of x = 15 in the Glabrata group presumably is either a doubled chromosome number minus one pair (x = 2 x 8 – 1) or else a combination of x = 8 and x = 7 genomes, perhaps originating through hybridization between an x = 8 plant and one from the Guttata group (thus x = 8 + 7). Compared to the Guttata group, the Madrensis and Glabrata groups have more eastern and southern distributions (central and southwestern USA through Mexico and into Andean South America).

1. **Madrensis group**
Subgroup A (*E. madrensis*, *E. pallens*, *E. calciphila*[*A], *E. pennellii*, *E. visibilis*[*A]). Perennial or annual, calyces 5-lobed or mostly 3-lobed; flowers small (allogamous or autogamous); western Mexico into southwestern USA. Base chromosome number = 16 (or 8).

Subgroup B (*E. chinatiensis*[*], *E. dentiloba*, *E. parvula*[*]). Perennial, mat-forming, calyces 5-lobed or with tendency toward 3-lobed; flowers relatively small, allogamous or autogamous; corolla lobes laciniate to fimbriate; southwestern USA and northwestern Mexico. Base chromosome number = 16 (or 8).

2. **Glabrata group**
Subgroup A - North American (*E. michiganensis*, *E. geyeri*[*], *E. inamoena*[*], *E. cordata*[*A], *E. regni*[*A], *E. utahensis*). Perennial and annual, rhizomatous or rooting at proximal nodes, annual and without rhizomes in *E. regni*, calyces not closing, flowers small and autogamous or (*E. michiganensis*) larger, chasmogamous and allogamous; central USA, Mexico. Base chromosome number = 15.

Subgroup B - South American (*E. acaulis*, *E. andicola*, *E. cuprea*, *E. depressa*, *E. glabrata*, *E. lacerata*, *E. lutea*, *E. nanandina*, *E. parviflora*, *E. pilosiuscula*, and perhaps others). Perennial and annual, rhizomatous or rooting at proximal nodes, calyces not closing; flowers chasmogamous and allogamous; South America (*E. glabrata* ranges into North America). Base chromosome number = 15.

3. **Guttata group**
Subgroup A, the Guttata subgroup (*E. corallina*, *E. grandis*, *E. arenicola*[A], *E. guttata*, *E. thermalis*[*A], *E. glaucescens*[A], *E. unmaculata*[A], *E. lagunensis*[A]). Perennial and annual; leaves oblong or elliptic to obovate, margins remotely toothed; flowers relatively large and chasmogamous and allogamous; western USA and northwestern Mexico. Base chromosome number = 14 (7), perhaps 16 (8). Reports for *E. corallina* are 2*n* = 48 and 56; these need to be restudied. Placement of *E. corallina* in the Guttata group rather than the Tilingii group is based on unpublished observations by Megan Peterson and John Willis.

Subgroup B, the Microphylla subgroup (*E. microphylla*[A], *E. marmorata*[A]). Annual, flowers large or variable in size, chasmogamous and allogamous; basal and proximal cauline leaves often purplish on one or both surfaces; central California (*E. marmorata*) and broader (*E. microphylla*). Base chromosome number = 14 (7).

Subgroup C, the Nasuta subgroup (*E. nasuta*[*A], *E. brevinasuta*[*A], *E. lacimata*[*A], *E. pardalis*[*A]). Annual, flowers small (cleistogamous or slightly open, autogamous; basal and proximal cauline leaves often purplish (*E. nasuta*, *E. laciniata*), flowers often produced at all nodes, proximal to distal; Sierra Nevada of USA (*E. laciniata*, *E. pardalis*) and broader (*E. nasuta*). Base chromosome number = 14 (7).

Subgroup D, the Arvensis subgroup (*E. arvensis*[*A], *E. brachystylis*[*A], *E. charlestonensis*[*A], *E. hallii*[A]). Annual, sometimes rooting at lower nodes (*E. arvensis*) but not rhizomatous; flowers often cleistogamous, all autogamous, produced from distal nodes; western USA. Base chromosome number = 14; *E. hallii* is reported as n = 16, perhaps through dysploidy. The Arvensis subgroup may constitute a single variable and widespread species (*E. arvensis*) with several peripheral isolates.

Subgroup E, the Nudata subgroup (*E. nudata*[A], *E. filicifolia*[A], *E. percaulis*[A]). Annual; leaf blades of reduced surface area; flowers produced mostly from distal nodes, chasmogamous, small and autogamous in *E. filicifolia* and *E. percaulis*; California. Base chromosome number = unknown.

Subgroup F, the Tilingii subgroup
Series 1 (*E. tilingii*, *E. minor*, *E. caespitosa*). Perennial; flowers large, chasmogamous and allogamous; filiform rhizomes profusely produced, mostly high elevation (except for *E. utahensis*); western USA. Base chromosome number = 14 (7) (*E. tilingii*: 2*n* = 28, 56).

Series 2 (*E. decora*, *E. scouleri*). Perennial; flowers large; rhizomes numerous; leaf margins closely toothed; styles densely hairy; Washington and Oregon. Base chromosome number = unknown.

Table 1. Infrasectional classification of *Erythranthe* sect. *Simiola*. Modified from Nesom (2012). Plants are allogamous and perennial unless otherwise noted. * = autogamous, [A] = annual duration.

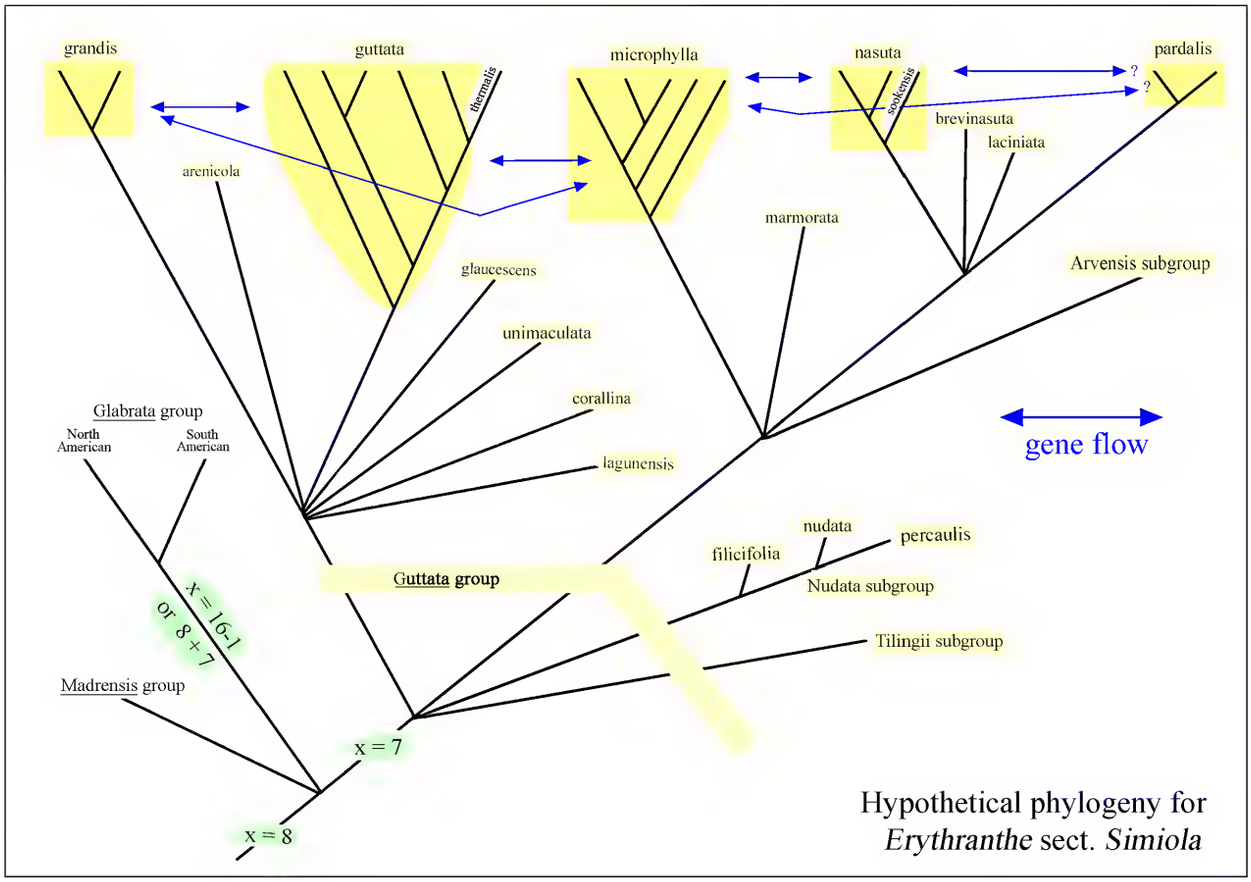

Figure 1. Hypothetical phylogeny of *Erythranthe* sect. *Simiola* (modified from Nesom 2013). The 50 species are divided into 3 main groups: Madrensis (x = 8), Glabrata (x =15), and Guttata (x = 7). Taxa of the Guttata group are highlighted in light yellow. Gene flow is inferred from morphological patterns. Extra branches within *E. grandis*, *E. guttata*, *E. microphylla*, *E. nasuta*, and *E. pardalis* indicate the existence of regional variants.

2. The Madrensis group. The species of Subgroup A are mostly restricted to montane regions of western Mexico and have a tendency to produce 3-lobed calyces. Morphological similarities between *E. madrensis* and *E. pallens* suggest that they may be sister species — they are broadly sympatric but apparently intergrade little if at all. In Subgroup A, *E. calciphila*, *E. pennellii*, and *E. visibilis* presumably are interrelated — they do not overlap in geography or morphology. Prior to 2012, *E. dentiloba*, *E. chinatiensis*, and *E. parvula* (Subgroup B) mostly had generally been identified collectively as *E. dentiloba* because of their laciniate to fimbriate corolla lobes, but each of the three has a distinct combination of biology and morphology and each is allopatric with both of the others. It seems a reasonable hypothesis that the range of an original, widespread, fimbriate-lobed species was fragmented into three geographic segments and at least two of them subsequently diverged evolutionarily. The disjunct population system of *E. dentiloba* in Baja California Sur might be expected to have significant genetic differences from the system in mainland Mexico but the two systems apparently have not diverged in morphology.

3. The Glabrata group. The division between subgroups A and B may prove to be arbitrary, but it seems likely that the species of the Andean cluster are more closely related among themselves. All chromosome counts for *Erythranthe cordata* (except one) have been $2n = 60$, a strong indication that it belongs in the Glabrata group. The chromosome number of the narrow endemic *E. regni* is unknown, but the species occurs on the range periphery of *E. cordata* and perhaps arose from a population of the latter. See comments on *E. utahensis* under the Tilingii group.

4. The Guttata group (the "*Mimulus guttatus* species complex," e.g., see Oneal et al. 2014, as inferred and extrapolated from their limited sampling of species) comprises about 26 species in the account here — all those above the 'x = 7' node on the phylogenetic diagram (Fig. 1). The present classification divides these 26 species into six subgroups (Guttata, Microphylla, Nasuta, Arvensis, Nudata, Tilingii).

5. *Erythranthe guttata* has often been referred to in molecular genetics literature as ancestor to the others of sect. *Simiola* or as the sister species to one or another species. Such observations are founded on phylogenetic study of a very small set of species or else they are assumptions without basis. The only statement (that I am aware of) explicitly in justification of ancestral status for *E. guttata* apparently is this: "Because of its wide geographical range and high levels of intraspecific genetic diversity it is likely that *Mimulus guttatus* is the progenitor of the other self-fertilizing species with restricted ranges" (Ferris et al. 2014, p. 9) — but this is flawed as a rationale (see Nesom 2014).

When the concept of ancestral "*Mimulus guttatus*" includes 2 or 3 or more different species, its meaning is ambiguous and interpretations of related speciation events are correspondingly ambiguous, misdirected, or meaningless. Similarly, assumptions of sister relationships between species of sect. *Simiola* often appear to be baseless and conclusions dependent on such assumptions also are invalid.

6. Evolutionary change from perennial (rhizomatous) to annual and from annual to perennial apparently has occurred multiple times among species of *Erythranthe* (as well as in the Phrymaceae as a whole). It is suggested here that rhizomes and stolons in *E. guttata*, *E. corallina*, and *E. grandis* and in the *E. tilingii* group probably are derived features, arising from ancestors of annual duration. All other x = 7 sect. *Simiola* species are annual, without rhizomes or stolons, as are most other species of *Erythranthe*. See related earlier comments (Nesom 2012).

Conceivably it is developmentally simple for lower branches to become rhizomelike or stolonlike by production of adventititous roots. Plants of *E. arvensis* and *E. cordata* characteristically are of annual duration (without rhizomes or stolons), but large plants in wet habitats sometimes become proximally decumbent or prostrate and develop adventitious roots at lower nodes and along the internodes. *Erythranthe glaucescens* is characteristically annual, but at least one rhizomatous population is known (Nesom 2012, p. 61; Taylor 2013) — the rhizomes (or runners) either arising independently from within the species or perhaps their genetic basis acquired by hybridization with *E. guttata*. Given the topology of Figure 1, it is likely that the rhizomes of *E. tilingii*, *E. guttata*, and *E. corallina* are not strictly homologous but rather have arisen independently in each instance. The distinctiveness of the numerous, very slender, rhizomelike, mostly above-ground runners originating from lowermost stem nodes characteristic of many populations of *E. guttata* in Colorado even suggests that they may have a different genetic basis than rhizomes of *E. guttata* from other regions.

7. The Arvensis subgroup may constitute a single variable and widespread species (*E. arvensis*) with several peripheral isolates. Annual duration, similar patterns of leaf shape and vestiture, and small autogamous flowers in this subgroup suggest a close relationship to *E. nasuta*. Occasional collections are encountered suggesting that gene flow occurs between *E. arvensis* and *E. nasuta*, although flowers of both species are autogamous.

8. All three species of the Nudata subgroup (*E. nudata*, *E. percaulis*, *E. filicifolia*) are annual in duration, completely glabrous to glabrate, and have slightly succulent leaves with prominently reduced surface area. All are narrow endemics and there is no morphological indication of genetic influence from any other species that might be suspected to have a close relationship. *Erythranthe nudata* and *E. percaulis* probably are sister species, with *E. percaulis* the more specialized.

9. The Tilingii subgroup (Series 1) can be interpreted as a widespread species divided, perhaps vicariantly, into three geographic units — *E. tilingii*, *E. caespitosa*, and *E. minor*. *Erythranthe decora* and *E. scouleri* are distinct from the *E. tilingii* trio and perhaps are sister species. There is no morphological indication of gene flow between species of the Tilingii subgroup and any others of the x = 7 lineage.

Erythranthe corallina was associated with *E. tilingii* in the 2012 account of sect. *Simiola* because of its slender rhizomes, similar to those of *E. tilingii*, but unpublished crossing data from John Willis and Megan Peterson suggest that it instead may be more closely related to the Guttata group. As a member of the Tilingii subgroup, it would be morphologically isolated.

Erythranthe utahensis, like *E. corallina*, is characterized by production of slender rhizomes and recently was associated with *E. tilingii* (Nesom 2012). It was originally described, however, as *Mimulus glabrata* var. *utahensis* Pennell (1935), emphasizing the calyx that remains open at maturity, and an allozyme analysis by Vickery (1990) placed *E. utahensis* as most similar to Andean taxa of the Glabrata group. The original assessment of relationship probably was correct. For the sect. *Simiola* revision, I examined vouchers at UT for chromosome counts of *E. utahensis* reported by Vickery: **2*n* = 28** (California, Mono Co.; Nevada, Mineral Co.; Utah, Juab Co.); **2*n* = 30** (Nevada, Elko Co. and White Pine Co.; Utah, Tooele Co. and Wayne Co.). A base number of x = 15 supports placement of *E. utahensis* with the Glabrata group; the counts of 2*n* = 28 should be reexamined — they might reflect a dysploid reduction or, particularly for the Californian populations, might suggest that those plants are better identified as a different taxon.

Molecular and genetic study

Oneal et al. (2014, p. 2857) are pessimistic regarding the potential for phylogenetic reconstruction in sect. *Simiola*.

> "Nesom (2012) argued that his hypothesized taxonomy of the species complex could be tested with a molecular phylogeny, but this is unlikely for two reasons. First and foremost, gene flow is widespread across the complex, and no phylogenetic methods currently exist which satisfactorily account for the confounding factor of hybridization (Eckert & Carstens 2008, Meng & Kubatko 2008, Liu *et al.* 2009), although one possible way forward is through new methods that evaluate population splits and mixtures in a tree-based framework (Pickrell & Pritchard 2012). Second, we have demonstrated convincingly that different regions of the genome, particularly the inversion, experience different patterns of introgression and shared ancestry. Together, these features suggest that the difficulty inherent in resolving relationships among the diverse members of the *M. guttatus* species complex is not merely a technical problem, but instead reflects the true nature of the speciation process, whereby clear genome-wide divergence does not occur until well after species are first identifiable."

Implication that knowledge of evolutionary processes ("the true nature of the speciation process") characterizing "the diverse members of the *M. guttatus* species complex" is at hand is a gross over-generalization, unjustified by any published research that I am aware of. The Oneal et al. sample apparently includes only about 10 species of the currently known 26 in the Guttata group of sect. *Simiola*, and their generalizations about the speciation process appear to be further restricted in purview, as they are based mostly on studies of interactions between *E. guttata* and *E. microphylla*, and in some cases *E. nasuta*. Judging from the geography and patterns of morphological variation for many (or most) of the remaining species, the guttata-microphylla model probably will not apply to them.

The Oneal et al. study (using a Bayesian clustering algorithm) includes *Erythranthe arvensis* (their "*Mimulus micranthus*" is a synonym), *E. caespitosa* (samples of "*Mimulus tilingii*" from Washington, as inferred), *E. guttata*, *E. laciniata*, *E. microphylla* (samples of annual "*Mimulus guttata*," as inferred), *E. minor* (samples of "*Mimulus tilingii*" from Colorado, as inferred), *E. nasuta*,

E. nudata, *E. pardalis* (their "*Mimulus cupriphilus*" is a synonym), and *E. tilingii* in the strict sense (collections from California and Oregon, as inferred). I am cited in the Acknowledgements as having "helped to confirm identification of many collection samples" but their identifications of "*M. guttatus*," "*M. micranthus*," "*M. cupriphilus*," and "*M. tilingii*" are not consistent with the way I would have identified them.

Well supported and plausible molecular phylogenies across many families have been reconstructed for species groups where gene flow occurs, and the possibility remains that reasonable hypotheses for the evolutionary history of the Guttata group and the larger sect. *Simiola* also can be formulated. Given the diversity of the group, there has not yet been any serious attempt to understand sect. *Simiola* phylogeny through either a molecular or genetic approach. Knowledge of species yet unsampled but obviously closely related to *E. guttata* and *E. microphylla* (Fig. 1) should be expected to provide insight into the phylogenetic positions of the latter two.

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KEY TO THE WILD DAFFODILS (*NARCISSUS*, AMARYLLIDACEAE) OF ALABAMA AND ADJACENT STATES

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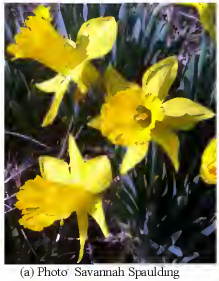
ABSTRACT

The genus *Narcissus* (Amaryllidaceae) is composed of about 26 species and four hybrids (*N.* ×*incomparabilis*, *N.* ×*intermedius*, *N.* ×*medioluteus*, *N.* ×*odorus*) that occur in the wild. Daffodils are native to Europe, western Asia, and northern Africa, but are introduced and naturalized elsewhere. In North America, six species (*N. bulbocodium*, *N. jonquilla*, *N. papyraceus*, *N. poeticus*, *N. pseudonarcissus*, *N. tazetta*) and the four previously mentioned hybrids have escaped cultivation. Each of these ten taxa occurs within the five-state region of Alabama, Georgia, Florida, Mississippi, and Tennessee. Keys, maps, photographs, and commentary are provided for each taxon.

Daffodils (*Narcissus* spp.) are bulbous perennials in the Amaryllidaceae (Amaryllis Family). *Narcissus* have showy white to yellow flowers with six tepals and a corona, which is also called a floral cup, tube, or crown. Flowers are either solitary or in clusters of 2 or more (Fig. 1).



(a) Photo: Savannah Spaulding

(b) Photo: Wayne Barger

Figure 1. (a) *Narcissus pseudonarcissus*, roadside, Calhoun Co., Alabama, 23 Feb 2014. (b) *Narcissus tazetta*, roadside, Fayette Co., Alabama, 2 Mar 2014.

All *Narcissus* are native to meadows and woods of Europe, north Africa and west Asia, with their distribution centered in the Mediterranean region (Webb 1980). Various common names including daffodil, narcissus, and jonquil are used to describe all or some members of the genus. The number of distinct species varies widely depending on how they are classified. According to Straley and Utech (2002), there are about 26 species, while other authors define more than 60 species (e.g., Ji & Meerow 2000).

Linnaeus (1753) named the genus and designated *Narcissus pseudonarcissus* as the type species. Haworth (1831) in his monograph divided the genus into 16 genera, but most authors place his genera within sections of *Narcissus* (Webb 1980). There are two possible derivations for the origin of the generic name. The first is said to be derived from the Greek work "*narkeo*, "to be stupified," referring to the narcotic alkaloids of the bulbs (Dweck 2002). Another interpretation is that the beautiful flower was named after Narcissus, the Greek mythological character, who fell in love with his reflection (Grieve & Leyel 1931). According to Martin (1987), the name 'daffodil" may possibly originate from the old English word, *affodyle*, which means 'that which comes early' or it may have been first named "d'asphodel" after the similar Asphodel flowers (*Asphodelus*).

Species and hybrids of *Narcissus* are widely used in gardens and landscapes. The cultivation of daffodils began before the end of the Sixteenth Century with collections originating from Spain and grown in the Netherlands (Pugsley 1933). Today there are thousands of named cultivars of *Narcissus* grouped in divisions such as trumpet daffodils, chalice-cupped daffodils, poet daffodils, bunch-flowered daffodils, double daffodils, and jonquils. Since daffodils have been cultivated for centuries, many wild populations that have naturalized are polymorphic due to horticultural selection (Webb 1980). Dearing and Griffiths (1930) declared that "there is scarcely a group of plants that has received so much attention at the hand of the hybridist or has been so much modified by culture and crossbreeding as the daffodil." *Narcissus* breeder George H. Engleheart (1895) unlocked the mystery of some of the crosses by taking on "the task of attempting to 'make' all these flowers over again, in order to determine with certainty their origin." Engleheart was successful in his quest and he discovered seven hybrid crosses for daffodils that were once thought to be species.

Naturalized daffodils are often undercollected and misidentified by field botanists. When making specimens of *Narcissus*, the collector should note number of flowers per scape (in the population), fragrance, tepal/corona color, and whether leaves are glaucous, green, flat, grooved, or round. Pugsley (1915) wrote that "while present-day gardeners have striven with energy to improve the Narcissus, very little botanical work on the genus has appeared."

Specimens were examined from various herbaria in the South (ALNHS, AMAL, AUA, BRIT, GA, FSU, JSU, MISS, TENN, TROY, UNA, and VDB). Maps (adapted from Lee 2012) were generated from over 200 recent collections by the authors, vouchered herbarium specimens from the institutions listed above, and the Alabama Plant Atlas (APA Editorial Committee 2014). Many North American treatments of *Narcissus* were utilized to assist in creating the following keys and determination of specimens. Publications used as references include the following: A Guide to Wild Daffodils (Blanchard 1990), Illustrated Flora of East Texas, Vol. 1 (Diggs et al. 2006), *Narcissus* species and wild hybrids (Meyer 1966), *Narcissus* of Arkansas (Serviss 2009), Flora of North America, Vol. 26 (Straley & Utech 2002), Keys to the Flora of Arkansas (Smith 1994), Flora of the Southern and Mid-Atlantic States (Weakley 2013), and Flora Europaea, Vol. 5 (Webb 1980).

Information on taxa is generally set up in the following format: **Number. Name** author(s) {derivation of specific epithets}. VERNACULAR NAME. Habitat; relative abundance in Alabama; flowering dates. Comments. [Distribution in adjacent states].

KEY TO *NARCISSUS* OF ALABAMA AND ADJACENT STATES

1. Flowers doubled, corona divided into numerous segments resembling tepals; stamens usually petaloid.

   2. Corona segments and tepals all about the same length; flowers yellow to greenish, corona segments frequently similar in color to tepals ..... **1. Narcissus pseudonarcissus**
   2. Corona segments shorter than tepals; flowers bicolored, corona segments usually bright orange and tepals pale yellow to creamy-yellow (petaloid stamens cream to yellow) ..... **3. Narcissus ×incomparabilis**

1. Flowers not doubled, corona undivided and distinct from tepals; stamens not petaloid.

   3. Corona as long as or longer than tepals; flowers yellow to orange-yellow (rarely white) and always solitary (1 per flowering stalk).

      4. Tepals ovate, triangular-ovate or suborbicular, more than 10 mm wide; leaves glaucous and greater than 5mm wide; corona cylindrical; anthers parallel to axis of tepals ..... **1. Narcissus pseudonarcissus**
      4. Tepals linear to narrowly lanceolate, less than 5 mm wide; leaves dark green and less than 3 mm wide; corona broadly funnel-shaped (infundibuliform), anthers perpendicular to axis of tepals..... **2. Narcissus bulbocodium**

   3. Corona distinctly shorter than the tepals; flowers yellow or white, 1–20 per flowering stalk.

      5. Corona ½ to ¾ as long as the tepals; hypanthial tube (just below perianth) distinctly widening towards the apex; tepals cream-colored, pale yellow or bright yellow and corona orange-yellow to golden yellow.

         6. Inflorescences always solitary; leaves mostly 7–11 mm wide, flat and not grooved; flowers fragrant and typically bicolored, tepals cream-colored or pale yellow and corona usually darker yellowish-orange..... **3. Narcissus ×incomparabilis**
         6. Inflorescences often umbellate (1)2(3–4)-flowered; leaves mostly 2–6 mm wide, thickened and grooved; flowers very fragrant and mostly uniform in color (corona sometimes slightly darker), tepals and corona both golden yellow to yellowish-orange ..... **4. Narcissus ×odorus**

      5. Corona much less than ½ as long as tepals; hypanthial tube mostly parallel-sided, though usually slightly flaring near the apex; tepals and corona yellow or white.

         7. Leaves thickened and either cylindrical (rush-like) or concave to folded, 2–9 mm wide; leaf surface green (not glaucous); tepals yellow.

            8. Leaves mostly round (terete), occasionally folded or grooved, 2–4 mm wide; flowers typically uniformly golden yellow, corona the same color as the tepals or only slightly darker; inflorescence 1–3 (4)-flowered..... **5. Narcissus jonquilla**
            8. Leaves concave (curved inward and somewhat flattened on one side), 3–10 mm wide; flowers with light lemon-yellow tepals and a distinctly darker yellow-orange corona; inflorescence 3–6 (7)-flowered ..... **6. Narcissus ×intermedius**

7. Leaves flat, not grooved 6–20 mm wide; leaf surface often glaucous; tepals white to cream (rarely yellow).

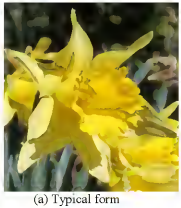
9. Inflorescence 1–3-flowered; tepals larger, usually 15–30 mm long; flowers fragrant or odorless.

10. Inflorescence always solitary (only one flower per stalk); corona bright yellow with a distinctive red, wavy rim (which often fades when dried); tepals white, usually 20–30 mm long; flowers fragrant ..... **7. Narcissus poeticus**
10. Inflorescence usually with 2 flowers (occasionally solitary or in 3's); corona usually yellow (rarely orange) but lacking a red rim (a reddish line is often present just below the rim); tepals cream-colored to white, usually less than 20 mm long; flowers not fragrant or only slightly so ..... **8. Narcissus ×medioluteus**

9. Inflorescence usually 4–15-flowered (occasionally with more or less flowers); tepals smaller, usually less than 15 mm long; flowers strongly fragrant.

11. Flowers concolored (entirely white), tepals and corona pure white (coronas may turn slightly coffee-colored as they age) ..... **9. Narcissus papyraceus**
11. Flowers bicolored, tepals white, cream or yellow and corona yellow to orange ..... **10. Narcissus tazetta**

1. Narcissus pseudonarcissus Linnaeus {false narcissus} — COMMON DAFFODIL; TRUMPET NARCISSUS (Figs. 1a & 2). Roadsides, fields, pastures, lawns, open woods, old home sites; throughout Alabama; common; February–March. This species is a native of Europe and is the most widely naturalized species in North America. It has escaped cultivation in the eastern half of the USA and also occurs in West Coast states (BONAP 2013). *Narcissus pseudonarcissus* is identified by its solitary flowers with a corona as long as or longer than the tepals. Double forms are often confused with double-flowered *N.* ×*incomparabilis*, but the tepals of *N. pseudonarcissus* are almost as long as the corona segments. [FL, GA, MS, TN]



(a) Typical form

(b) Double yellow form

(c) Double green form

Figure 2. *Narcissus pseudonarcissus*, (a) Roadside, Blount Co., Alabama, 27 Feb 2014. Photo: Wayne Barger. (b) Herbarium specimen (AMAL), *Spaulding & Taylor 13881*, roadside, Cleburne Co., Alabama, 15 Mar 2014. (c) Cultivated specimen, Greene Co., Alabama, 22 Feb 2010. Photo: Richard Buckner.

2. Narcissus bulbocodium Linnaeus {bulb with sheep skin} — HOOP-PETTICOAT DAFFODIL (Fig. 3).

Roadsides, disturbed woods and woodland borders; upper Coastal Plain; rare; March–April. *Narcissus bulbocodium* was recently collected in 2014 by Brian Keener in Livingston, Alabama (Sumter County) and is new to the state (Kral et al. 2011). This taxon has also been documented from Moore County, North Carolina by Bruce Sorrie and reported to occur in Lincoln Parish, Louisiana (BONAP 2013). This species is easily identified by its solitary yellow flowers that have narrow tepals and a big funnel-shaped corona. *Narcissus bulbocodium* is native to open and rocky areas of Portugal, Spain, and southwest France (Webb 1980).

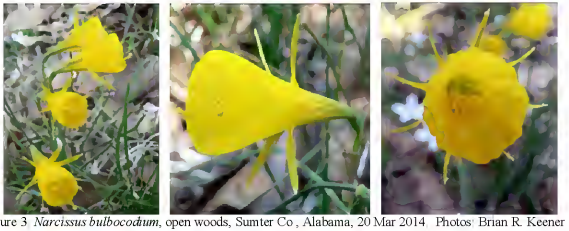
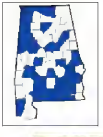
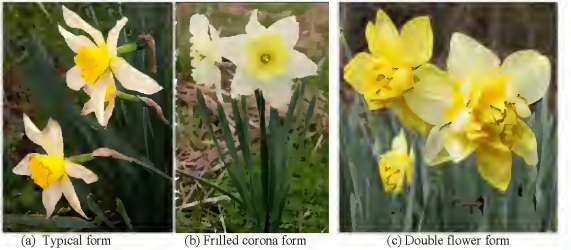


Figure 3. *Narcissus bulbocodium*, open woods, Sumter Co., Alabama, 20 Mar 2014. Photos: Brian R. Keener

3. Narcissus ×incomparabilis P. Miller {incomparable} [*N. poeticus* × *N. pseudonarcissus*] — NONESUCH DAFFODIL; PEERLESS DAFFODIL (Fig. 4). Roadsides, pastures, woodland borders, railroad tracks; throughout Alabama; frequent; February–April. This sterile taxon is native to France and is thought to be a natural hybrid (Webb 1980). This hybrid is sometimes mistaken for *Narcissus pseudonarcissus* because it has solitary, yellowish flowers, but *N. ×incomparabilis* has a corona only about half the length of the tepals. *Narcissus poeticus* is also similar but has a shorter corona with a red rim. [FL, GA, MS, TN]





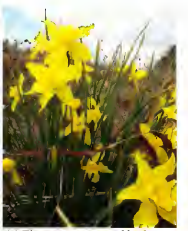
(a) Typical form (b) Frilled corona form (c) Double flower form

Figure 4. *Narcissus ×incomparabilis*. (a) Roadside, Green Co., Alabama, 19 Mar 2014. (b) Field, Marengo Co., Alabama, 6 Mar 2014. (c) Roadside, Wilcox Co., Alabama, 7 Mar 2014. Photos: Spaulding and Barger (b & c)

4. Narcissus ×odorus Linnaeus {scented} [*N. jonquilla* × *N. pseudonarcissus*] — CAMPERNELLE JONQUIL, SWEET-SCENTED JONQUIL (Fig. 5). Roadsides, fields, pastures and other open disturbed areas; throughout Alabama; common, February–April. This common hybrid is sterile and spreads through asexual means. *Narcissus ×odorus* is often confused with *N. pseudonarcisssus*, but is usually multi-flowered, has golden yellow tepals that are distinctly longer then the corona, and grooved, narrow leaves that often overtop the flowers. *Narcissus ×odorus* is also similar to *N. ×intermedius* and *N. jonquilla*, but their flowers are much smaller. [GA, MS, TN]

(a) Paired flowers

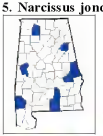
(b) Concave leaves

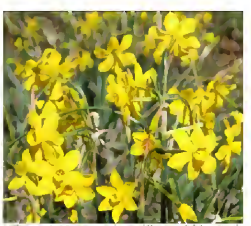


(c) Flowers overtopped by leaves

Figure 5. *Narcissus ×odorus*. (a & b) Roadside, Lowndes Co., Alabama, 6 Mar 2014. Photos: Wayne Barger. (c) Old field, Calhoun Co., Alabama, 14 Mar 2014. Photo: Dan Spaulding.

5. Narcissus jonquilla Linnaeus {Spanish name for *Juncus*} — JONQUIL, APODANTHUS DAFFODIL (Fig. 6). Roadsides and lawns; throughout Alabama; infrequent, February – April. The species has round (sometimes grooved) hollow stems that resemble rushes (*Juncus*) and are usually no more than 4mm wide. The name jonquil is derived from European names for rush (Martin 1987). Many specimens labeled as *N. jonquilla* were annotated to *N. ×intermedius*, which has wider, concave leaves and flowers that are bicolored rather than uniformly golden yellow. *Narcissus ×odorus* is also similar, but has much larger flowers with a longer corona. [MS, TN]





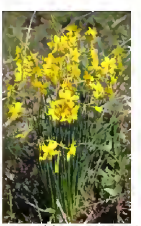


Figure 6. *Narcissus jonquilla*, roadside, Covington Co., Alabama, 20 Mar 2014. Photos: Wayne Barger.

6. Narcissus ×intermedius Loiseleur {intermediate} [*N. jonquilla* × *N. tazetta*] — STAR DAFFODIL; STAR JONQUIL (Fig. 7). Roadsides, fields, power line right-of-ways, and old home sites; common on the coastal plain, infrequent in the Appalachian Highlands; February–March. This sterile hybrid spreads through asexual production of bulblets (Nesom 2010). It is often confused with *Narcissus jonquilla*, but *N. ×intermedius* can be distinguished by its channeled, concaved leaves that are mostly over 4 mm wide and has a darker orange corona contrasting with lighter yellow tepals. This hybrid's thick leaves, which are swollen and grooved, are intermediate between its parents, *N. jonquilla* and *N. tazetta*. [GA, MS]

Figure 7 *Narcissus jonquilla*, roadside, Macon Co., Alabama, 7 Mar 2014 Photos: Wayne Barger

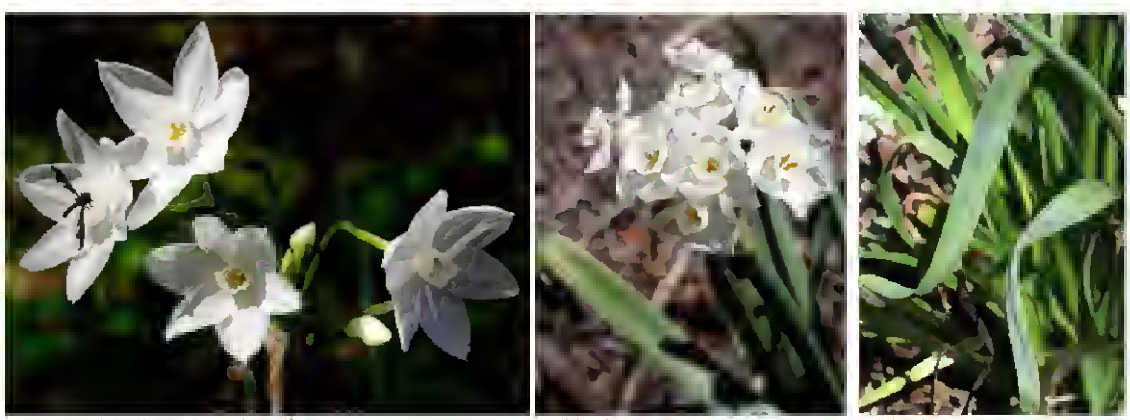
7. Narcissus poeticus Linnaeus {of the poets} — POET'S NARCISSUS; PHEASANT'S-EYE DAFFODIL (Fig. 8). Roadsides and old home sites; mostly northern Alabama; rare; March–April. This daffodil is introduced from Europe and has naturalized in the eastern half of USA and Canada, but appears to be more common further north (BONAP 2013). Almost all the plants identified as this species from Alabama were actually the hybrid *Narcissus ×medioluteus*, which can have solitary flowers but lacks the distinctive red-margined rim on the corona. The flowers of *Narcissus poeticus* are a little larger than *N. ×medioluteus*, but they are always solitary. [GA, MS, TN]

Figure 8 *Narcissus poeticus*, roadside, Lauderdale Co., Alabama, 20 Mar 2014 Photos: Wayne Barger

8. Narcissus ×medioluteus P. Miller {medium-yellow} [*N. poeticus* × *N. tazetta*] — PRIMROSE-PEERLESS; TWIN-SISTERS, TWO-FLOWER NARCISSUS (Fig. 9). Fields, roadsides, road banks, pastures, and other disturbed areas; chiefly northern half of Alabama, common, March–April. Flowers resemble *Narcissus poeticus* but are slightly smaller and usually in pairs, though they can be solitary or in threes. It lacks the red wavy margin on the rim of the corona, though it may have a thin reddish-brown ring around the upper portion of the corona. It differs from *Narcissus papyraceus* and *N. tazetta* by having fewer flowers (3 or less) and often has a small amount of yellow coloration at the base of the tepals adjacent to corona. [GA, MS, TN]

Figure 9. *Narcissus ×medioluteus*, old field, Calhoun Co., Alabama, 28 Apr 2014. Photos: Dan Spaulding

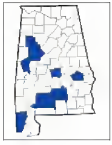
9. Narcissus papyraceus Ker-Gawler {paper-like} — PAPER-WHITE NARCISSUS (Fig. 10). Roadsides, fields, disturbed sites; coastal plain, infrequent; November–March. This species is native to southern Europe and the Mediterranean region. It is reported for California, Texas and Louisiana (BONAP 2013). *Narcissus tazetta* is similar, but has a yellow or orange corona. Flowers are extremely fragrant and bulbs are often forced to bloom in winter as a temporary houseplant. Several subspecies of *N. papyraceus* are recognized by various authors and are separated by flower size, texture, and whether the leaves are glaucous or green (Webb 1980).



(a) Photo: Fred Nation (b) Photo Wayne Barger (c) Photo Wayne Barger

Figure 10. *Narcissus papyraceus* (a) Roadside, Baldwin Co., Alabama, 4 Jan 2011. (b & c) Inflorescence and leaves, roadside, Elmore Co., Alabama, 14 Mar 2014

10. Narcissus tazetta Linnaeus {small cup} — BUNCH-FLOWER DAFFODIL; CREAM NARCISSUS



(Figs. 1b & 11). Roadsides, fields, and old home sites; chiefly coastal plain; infrequent; February–April. This species is native to Western Europe, Mediterranean region, and southwest Asia. *Narcissus tazetta* is a strongly polymorphic species. Flower size, number and color are variable, which may due to many years in cultivation. All specimens of *N. tazetta* examined from Alabama and adjacent states had 4 to 15 flowers per stalk. According to Diggs et al. (2006), the inflorescences of *N. tazetta* usually have about 2–8(-15) flowers per stalk, whereas *N. papyraceus* have (2-)5–15(-20) flowers per stalk. Webb (1980) recognized three subspecies of *N. tazetta* in Europe: subsp. *tazetta* has pure white tepals; subsp. *italicus* (Ker-Gawler) Baker has cream colored tepals; and subsp. *aureus* (Loiseleur) Baker has golden yellow tepals with an orange corona. Individuals with white tepals are the most common form of this species in the South. It is sometimes difficult to distinguish white tepal forms of *N. tazetta* from *N. papyraceus* when dried because the colored corona of *N. tazetta* can fade. Some previous authors have considered the two species synonymous because of their similarity on herbarium sheets (Straley & Utech. 2002). Fresh specimens of *N. tazetta* are easily separated by the distinct yellow corona, which contrasts with the lighter tepals. The white tepal form can also be confused with *Narcissus ×medioluteus*, but *N. tazetta* typically has more than three flowers per stalk and lacks any yellow coloration at the base of their tepals. The yellow tepal form of *Narcissus tazetta* has recently been documented from Alabama and is reported to occur in other southeastern states. This color form can be confused with *N. ×intermedius*, but *N. tazetta* has completely flat leaves. [MS]

(a) White tepal form

(b) Close-up of inflorescence

(c) Yellow tepal form

Figure 11. *Narcissus tazetta*. (a) Roadside, Macon Co., Alabama, 20 Feb 2014. Photo: Wayne Barger (b) Roadside, Autauga Co., Alabama, 7 Mar 2014. Photo: Wayne Barger. (c) Herbarium specimen (AMAL), *Horne 1569*, Mobile Co., Alabama, 13 Mar 2011.

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THE GENUS *BAPTISIA* (FABACEAE) IN ALABAMA

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ABSTRACT

The primary objectives of this project were to determine which species of *Baptisia* (Fabaceae) occur in Alabama and to report the county distribution of each. *Baptisia*, known commonly as wild or false indigo, is recognized as consisting of seven species in Alabama. The most common species are *Baptisia alba, B. bracteata,* and *B. megacarpa.* The less common species are *B. lanceolata* and *B. albescens*. The least common species are *B. australis* and *B. perfoliata.* The dichotomous key and descriptions we present are modifications from earlier authors; however, all measurements are based on morphological features of the vegetative and reproductive structures of the more than 200 specimens studied during this project. Data for the county-level distribution maps were compiled entirely from herbarium vouchers.

Baptisia, commonly known as wild or false indigo, consists of 18 species, 7 infraspecific taxa, and 6 hybrids confined to the eastern USA and Canada (NatureServe 2013). Of these, 15 species have been reported from the southeastern USA (Isely 1990) and eight species and one infraspecific taxon have been reported from Alabama (Kral et al. 2011).

The genus *Baptisia* Vent. is a member of the legume family Fabaceae (Leguminosae), tribe Thermopsideae, which includes six genera and approximately 45 species scattered through the Mediterranean and eastern North America (Turner 1981). More recently, results based on nuclear ribosomal DNA internal transcribed space (ITS) sequences suggest the Thermopsideae could be reduced to four core genera, *Anagyris*, *Baptisia*, *Pipthanthus*, and *Thermopsis*, which are clustered to form a strong clade (Wang et al 2006).

Two taxa of *Baptisia*, *B. australis* (L.) R. Br. and *B. megacarpa*, have received a state and global rank of G5T2S1, G2S2, respectively (Alabama Natural Heritage Program 2013). *Baptisia perfoliata* (L.) R. Br. ex Ait. f., although it has no state or global rank, is the rarest *Baptisia* in the state, known from only Sumter County, which is the westernmost county in the state. The closest population is Laurens County, Georgia, some 500 km to the east (USDA, NRCS 2013).

The primary objectives of this study were to determine which species of *Baptisia* occur in Alabama and report the county-level distribution of each. Additional goals included providing a dichotomous key, species descriptions, and illustrations for the taxa of *Baptisia* found to occur in Alabama.

Material and methods

Data for the distribution maps were gathered from more than 200 plant specimens deposited in the herbaria of Troy University (TROY), Alabama Natural History Survey (ALNHS), J.D. Freeman (AUA), The University of Alabama (UNA), The University of South Alabama (USAM), The University of West Alabama (UWAL), Jacksonville State University (JSU), Anniston Museum

of Natural History (AMAL), University of North Alabama (UNAF), and Vanderbilt University (VDB), which is housed at the Botanical Research Institute of Texas in Fort Worth.

The dichotomous key is a modification of Isely (1990) and Weakley (2012); however, all measurements are based on morphological features of the vegetative and reproductive structures of the plants examined during this project. Descriptions for each taxon are based on those of Larisey (1940) and Isely (1990), with modifications incorporating measurements taken from the specimens studied. The lists of specimens examined are limited to one record from each county.

Herbarium specimens were initially divided into groups based on overall morphological similarity and the species concept established by Larisey (1940), Isely (1990), and Weakley (2012). Morphological measurements were then made from selected specimens of each group. Field studies were also conducted to observe the species in their natural habitats and make personal collections.

Results

Seven species of *Baptisia* occur in Alabama. The most common species in the state is *Baptisia alba* (L.) Vent., represented in 25 counties. *Baptisia bracteata* Muhl. ex Ell. is represented in 13 counties and *B. megacarpa* Chapm. ex Torr. & Gray is represented in 10 counties. *Baptisia lanceolata* (Walt.) Ell. is represented in six counties and *B. albescens* Small is represented in 5 counties. The least common species are *B. australis* (L.) R. Br. (1 county) and *B. perfoliata* (L.) R. Br. ex Ait. f. (1 county).

TAXONOMIC TREATMENT OF *BAPTISIA* IN ALABAMA

Baptisia Vent., Dec. Gen. Nov. 1808.
Crotalaria Dill. ex L., Gen. Pl., ed. 1, 218. 1737, in part.
Sophora L., Gen. Pl., ed. 1, 125. 1737, in part.
Podalyria Lam., Illust. 2: 454. pl. 327, fig. 3,4. 1793, in part.
Crotalopsis Michx. ex DC., Prodr. 2: 100. 1825, in syn.
Eaplosia Raf., New Fl. 2: 51. 1837 ("1836").
Lasinia Raf., New Fl. 2: 48. 1837 ("1836").
Pericaulon Raf., New Fl. 2: 50. 1837 ("1836").
Ripasia Raf., New Fl. 2: 48. 1837 ("1836").

Perennial herbs. **Stems** ascending or erect, branched, glabrous or pubescent. **Leaves** alternate, palmately trifoliate (upper ones bifoliolate or unifoliolate) or all unifoliolate, sessile or petiolate; leaflets entire, elliptic, elliptic-lanceolate, ovate-elliptic, ovate-lanceolate, oblanceolate to orbicular, stipules absent, caducous or persistent. **Inflorescence** terminal racemes, erect, ascending to arching or flowers 1–2 in leaf axis, bracts small, caducous or subfoliaceous and persistent, bracteoles absent. **Calyces** campanulate 4–8 mm long, lobes 4, subequal, shorter or exceeding tube, pedicels 2–30 mm long; corolla papilionaceous, 13–30 mm long, white, cream, yellow, or violet to blue; androecium monadelphous, stamens 10; style longer than ovary, distally glabrous. **Fruits** stipitate, inflated, lanceolate to globose, coriaceous to woody.

KEY TO THE ALABAMA SPECIES OF *BAPTISIA*

1. Leaves unifoliolate, perfoliate ..... 1. **Baptisia perfoliata**
1. Leaves trifolioate, sessile or petiolate.

2. Flowers lavender or blue ..... 2. **Baptisia australis**
2. Flowers white, cream, or yellow.

3. Bracts persistent; pedicels 15–30 mm long; mature racemes arching 3. **Baptisia bracteata**
3. Bracts caducous; pedicels 2–10 mm long; mature racemes ascending or erect.

4. Flowers yellow.

5. Legumes woody, pubescent, 10–25 mm long, 8–12 mm wide; petioles 0.4–12 mm long ..... 4. **Baptisia lanceolata**
5. Legumes thinly-coriaceous, glabrous, 30–40 mm long; petioles 15–20 mm long ..... 5. **Baptisia megacarpa**

4. Flowers white.

6. Calyces 4.5–6.5 mm long; corollas 13–18 mm long; legumes yellow-brown at maturity ..... 6. **Baptisia albescens**
6. Calyces 7–8 mm long; corollas 20–25 mm long; legumes black at maturity ..... 7. **Baptisia alba**

1. **Baptisia perfoliata** (L.) R. Br. in Ait., Hort. Kew., ed. 2, 3: 5. 1811.
Crotalaria perfoliata L., Sp. Pl. 2: 714. 1753.
Sophora perfoliata Walt., Fl. Car. 135. 1788.
Rafnia perfoliata Willd. in L., Sp. Pl. ed. 4, 3: 949. 1800.
Podalyria perfoliata Michx., Fl. Bor. Amer. 1: 263. 1803.
Pericaulon perfoliatum Raf., New. Fl. N. Amer. 2: 51. 1836.
Pericaulon cordatum Raf., New Fl. N. Amer. 2: 51. 1836.

Perennial herbs. **Stems** arching, branched, glabrous, somewhat glaucous. **Leaves** simple, perfoliate, leathery, orbicular to ovate-elliptic, 5–10 cm long, 3–8 cm wide, stipules absent. **Flowers** axillary, solitary. **Calyces** 6–7 mm long, peduncles 4–7 mm long; corolla 13–15 mm long, bright yellow. **Fruits** ovoid to globose, coriaceous, glabrous, brown, 1–1.5 cm long. Figure 1.

Native of Florida, Georgia, and South Carolina. Habitat and distribution in Alabama: dry soil at edge of longleaf pine woods; west-central Alabama.

Specimen examined. Sumter Co.: *Keener 2656*, 17 Jun 2005 (TROY).

2. **Baptisia australis** (L.) R. Br. in Ait., Hort. Kew, ed. 2, 3: 6. 1811.
Sophora australis L., Syst. Veg., ed. 14. 391. 1784.
Sophora caerulea Trew, Pl. Rar. 6, pl. 14. 1779.
Podalyria australis Willd. in L., Sp. Pl., ed. 4, 2: 503. 1799.
Baptisia exalata Sweet, Br. Fl. Gard. 1: pl. 97. 1825.
Baptisia viscolor Lodd., Bot. Cab. 12: pl. 1144. 1826.
Baptisia confusa Sweet ex G. Don, Gen. Syst. [Hort. Brit.], ed. 2, 123. 1830.
Ripasia cerulea Raf., New. Fl. N. Amer. 2: 48. 1837 ("1836").
Baptisia caerulea Michx. in Eaton & Wright, Man. N. Amer. Bot., ed. 8, 154. 1840.
Baptisia australis var. *aberrans* Larisey, Ann. Mo. Bot. Gard., 27: 206. 1940.

Perennial herbs. **Stems** erect, branched, glabrous, somewhat glaucous. **Leaves** trifoliate, petioles 0.2–1.2 cm long; leaflets obovate to obovate-lanceolate, 4–8 cm long, 1.5–3 cm wide, stipules persistent. **Inflorescence** terminal, arching, loosely flowered, 2–5 cm long, bracts caducous. **Calyces** 9–12 mm long, pedicels 5–10 mm long; corolla 25–30 mm long, lavender or blue. **Fruits** ovoid to globose, coriaceous, glabrous, brown, 1–1.5 cm long. Figure 2.

Native of central and eastern USA. Habitat and distribution in Alabama: river banks and gravel bars; central Alabama.

Specimen examined. Bibb Co.: *Allison 8226*, 30 Apr 1994 (UNA).

3. **Baptisia bracteata** Muhl. ex Ell., Sketch Bot. S. Car. & Ga. 1: 469. 1821.
Podalyria bracteata Muhl., Cat. Pl. Amer. Sept. 42. 1815, nomen subnudum.
Lasmia bracteata Raf., New. Fl. N. Amer. 2: 50. 1837 ("1836").
Baptisia leucophaea Nutt. ex Chapm., Fl. South. U.S., ed. 1, 112. 1860.
Baptisia saligna Greene, Leafl. Bot. Obs. 2: 84. 1910.

Perennial herbs. **Stems** erect, branched, glabrous to pubescent. **Leaves** trifoliate, petioles 0.3–1.2 cm long; leaflets oblanceolate to obovate or elliptic-obovate, 5–10 cm long, 2–3.5 cm wide; stipules persistent with those of medial leaves foliaceous. **Inflorescence** axillary, arching, secund, 10–20 cm long, bracts persistent. **Calyces** 7–10 mm long, pedicels 15–30 mm long; corolla 18–25 mm long, cream or yellow. **Fruits** elliptic, woody, subappressed-pubescence, brown, 3–5 cm long. Figure 3.

Native of southeastern USA. Habitat and distribution in Alabama: dry pine and oak woods, roadsides; central and northeastern Alabama.

Specimens examined. Calhoun Co.: *Hansen 2099*, 18 Apr 2006 (TROY). Cherokee Co.: *Barger 25*, 25 Apr 2007 (TROY). Chilton Co.: *Diamond, 15467*, 16 Jun 2005 (TROY). Clay Co.: *Haynes, 9054*, 30 Apr 1977 (UNA). Cleburne Co.: *Keener 3467*, 8 Apr 2007 (UWAL). Coosa Co.: *Keener 4348*, 28 Apr 2008 (UWAL). DeKalb Co.: *Searcy s.n.*, 30 Apr 1966 (AUA). Etowah Co.: *Spaulding & Soehren 10502*, 1 May 1998 (JSU). Jefferson Co.: *Wright s.n.*, 15 Apr 1965 (AUA). Lee Co.: *Davis s.n.*, 27 Apr 1957 (AUA). Shelby Co.: *Whetstone & Ballard 16293*, 4 Apr 1993 (JSU). St. Clair Co.: *Bradshaw 81*, 9 Apr 1977 (UNA). Talladega Co.: *Hilton 159*, 15 Apr 1994 (AUA).

4. **Baptisia lanceolata** (Walt.) Ell., Sketch Bot. S. Carolina 1: 467. 1817.
Sophora lanceolata Walt., Fl. Car. 135. 1788.
Podalyria uniflora Michx., Fl. Bor. Amer. 1: 263. 1803.
Baptisia uniflora (Michx.) Nutt., Gen. N. Amer. Pl. 1: 281. 1818.
Lasmia reticulata Raf., New Fl. N. Amer. 2: 48. 1836 [1837].
Baptisia elliptica Small, Fl. S.E. U.S., 559, 1331. 1903.
Baptisia elliptica var. *tomentosa* Larisey, Ann. Mo. Bot. Gard. 27(2): 150. 1940.
Baptisia lanceolata var. *tomentosa* (Larisey) Isely, Brittonia 30: 471. 1978.
Baptisia lanceolata var. *elliptica* (Small) B.L. Turner, Phytologia 88: 256. 2006.

Perennial herbs. **Stems** erect, branched, glabrous or appressed pubescence. **Leaves** trifoliate, petioles 0.4–1.2 cm long; leaflets obovate, elliptic, lanceolate or oblanceolate, 5–13 cm long, 2–3.5 cm wide, stipules caducous. **Inflorescence** axillary or terminal, erect, 3–6 cm long; bracts persistent. **Calyces** 8–10 mm long, pedicels 2–10 mm long; corolla 20–25 mm long, yellow. **Fruits** suborbicular to lanceolate, woody, glabrous or with remnants of pubescence, black, 1–2.5 cm long. Figure 4.

Native of southeast USA. Habitat and distribution in Alabama: dry pine and oak woods, roadsides; extreme southern Alabama.

Specimens examined. Baldwin Co.: *Kenner 2899*, 5 May 2006 (TROY). Covington Co.: *Diamond 20560*, 9 Apr 2009 (TROY). Escambia Co.: *Diamond 13204*, 19 May 2002 (TROY).

Geneva Co.: *Kral, 34538*, 26 Apr 1969 (AUA). Houston Co.: *MacDonald 8627*, 7 May 1995 (UNA). Mobile Co.: *Mohr s.n.*, Jun 1879 (UNA).

5. **Baptisia megacarpa** Chapm. ex Torr. & Gray, Fl. N. Amer. 1: 386. 1840.
Baptisia riparia Larisey, Ann. Missouri Bot. Gard. 27: 192, t. 26(1). 1940.
Baptisia riparia var. *mintma* Larisey, Ann. Missouri Bot. Gard. 27: 193, t. 26(2). 1940.

Perennial herbs. **Stems** erect, branched, glabrous. **Leaves** trifoliate, petioles 1.5–2 cm long; leaflets broadly elliptic, 4–8 cm long, 1.5–4 cm wide, stipules caducous. **Inflorescence** terminal and axillary, erect, 7–15 cm long, bracts caducous. **Calyces** 8–10 mm long, pedicels 12–15 mm long; corolla 17–22 mm long, yellow. **Fruits** ellipsoid to ovoid, bladdery-inflated, thinly-coriaceous, glabrous, tan to brown, 3.5–5 cm long. Figure 5.

Native of southeastern USA. Habitat and distribution in Alabama: dry pine and oak woods, moist ravines, stream edges and roadsides; south central and southeastern Alabama.

Specimens examined. Bibb Co.: *Kenner 4505*, 27 May 2008 (UWAL). Bullock Co.: *Diamond 24009*, 9 May 2013 (TROY). Crenshaw Co.: *Diamond 11866*, 16 Jul 2000 (TROY). Coosa Co.: *Diamond 24441* 11 Aug 2013 (TROY). Escambia Co.: *Brittain 270,* 21 May 1995 (TROY). Lee Co.: *Sessler 174,* 21 May 1975 (AUA). Macon Co.: *Redmond 125*, 24 May 1970 (AUA). Montgomery Co.: *Harper 4114*, 7 May 1949 (UNA). Pike Co.: *Diamond 21975,* 26 Apr 2011 (TROY). Tallaposa Co.: *Schotz 2014,* 10 May 2006 (AUA).

6. **Baptisia albescens** Small, Fl. S.E U.S., ed. 1, 600, 1331. 1903. 1800.

Perennial herbs. **Stems** erect, branched, sparsely pubescent when young, becoming glabrous. **Leaves** trifoliate, petioles 0.5–1.8 cm long; leaflets elliptic-lanceolate to obovate, 2–6 cm long, 0.5–1.5 cm wide, stipules caducous. **Inflorescence** terminal, erect, 15–40 cm long, bracts caducous. **Calyces** 5–8 mm long, pedicels 6–10 mm long; corolla 13–17 mm long, white. **Fruits** cylindrical to oblong-lanceolate, coriaceous, glabrous, yellow-brown, 2–3.5 cm long. Figure 6.

Native of southeast USA. Habitat and distribution in Alabama: dry pine woods, sandy areas and roadsides; southeastern Alabama.

Specimens examined. Barbour Co.: *Diamond 21985*, 26 Apr 2011 (TROY). Bullock Co.: *Barger 278*, 5 May 2011 (ALNHS). Houston Co.: *Mohr 1165*, 27 May 1971 (TROY). Lee Co.: *Kral 62292A,* 11 Jul 1978 (AUA). Russell Co.: *Diamond 9122*, 1 May 1994 (AUA).

7. **Baptisia alba** (L.) Vent., Dec. Gen. Nov. 1808.
Crotalaria alba L., Sp. Pl. 2: 716. 1753.
Sophora alba L., Syst. Nat., ed. 12, 2: 287. 1767.
Podalyria alba Willd. in L., Sp. Pl., ed. 4, 2: 503. 1799.
Baptisia albiflora Raf., New Fl. N. Amer. 2: 47. 1836 [1837].
Baptisia alba var. *macrophylla* (Larisey) Isely, Sida 11: 435. 1986.

Perennial herbs. **Stems** erect, branched, glabrous, glaucous. **Leaves** trifoliate, petioles 1–2 cm long; leaflets elliptic-obovate to oblanceolate, 2–6 cm long, 0.8–2.5 cm wide, stipules caducous. **Inflorescence** terminal, erect, 25–50 cm long, bracts caducous. **Calyces** 7–8 mm long, pedicels 3–10 mm long; corolla 20–25 mm long, white. **Fruits** cylindrical to ellipsoid to ellipsoid-cylindric, coriaceous, glabrous, black, 2–5 cm long. Figure 7.

Native of central and southeastern USA. Habitat and distribution in Alabama: dry pine and woods, open fields, floodplains and roadsides; throughout Alabama.

Specimens examined. Bibb Co.: *Moore s.n.*, 9 Apr 1955 (AUA). Butler Co.: *Diamond 17393*, 18 Apr 2007 (TROY). Cherokee Co.: *Whetstone 10000*, 6 May 1980 (JSU). Choctaw Co.: *Tippins s.n.*, 28 Apr 1952 (AUA). Clark Co.: *Henderson 23*, 4 May 1981 (AUA). Colbert Co.: *Whetstone 4349*, 6 Jun 1975 (JSU). Conecuh Co.: *Diamond 8693*, 26 Jun 1993 (AUA). Covington Co.: *Jones 539*, 7 Apr 1960 (AUA). Dale Co.: *Diamond 8223*, 3 May 1992 (AUA). Fayette Co.: *Haynes 9942*, 30 Apr 1999 (UNA). Green Co.: *Keener 2649*, 28 Apr 2005 (TROY). Henry Co.: *Diamond 18965*, 13 Apr 2008 (TROY). Jackson Co.: *Brodeur 1822*, 18 May 1999 (JSU). Macon Co.: *Lancaster 164*, 8 Apr 1974 (AUA). Madison Co.: *Curley s.n.*, 19 May 1973 (JSU). Morengo Co.: *England 1952*, 17 Apr 2009 (UWAL). Mobile Co.: *Mohr s.n.*, Jun 1867 (UNA). Montgomery Co.: *Hutto 206*, 12 Apr 1974 (AUA). Morgan Co.: *Keener 2601*, 18 Apr 2003 (TROY). Pickens Co.: *Kral 46783*, 28 May 1972 (JSU). Pike Co.: *Diamond 12408*, 29 Apr 2001 (TROY). Russell Co.: *Gil 2001-135*, 25 Apr 2002 (AUA). Sumter Co.: *Harris s.n.*, 25 May 2003 (UWAL). Tuscaloosa Co.: *Spaulding 11020*, 21 Apr 2001 (UNA). Washington Co.: *Zebryk 8575*, 29 May 2004 (USAM).

DISCUSSION

In Alabama, *Baptisia* is a conspicuous taxon of open pine or oak woodlands, sandhills, slopes, cedar glades, barrens, pastures, and roadsides (Isely 1990). The state and global ranked taxon *B. australis* has a more restricted habitat, occurring only on river banks and gravel bars. The entire plant in all species of *Baptisia* contains toxic properties, which include various alkaloids and glycosides (Gibbons et al. 1990).

A combination of morphological characteristics can be used to differentiate the seven species of *Baptisia* in Alabama. *Baptisia perfoliata* and *B. australis* are the most easily recognized taxa. *Baptisia perfoliata* has simple, perfoliate leaves, whereas, the remaining taxa have trifolioate leaves. *Baptisia australis* has lavender or blue flowers and the remaining taxa have white or cream colored to yellow flowers. *Baptisia bracteata* is unique in having large and persistent stipules, 15–40 mm long, bracts 5–30 mm long and pedicels 15–30 mm long. The remaining four taxa have stipules less than 5 mm long or caducous, persistent bracts, 2–5 mm long and pedicels 2–10 mm long. The foliage of *B. megacarpa* and *B. alba* are similar, but *B. megacarpa* differs in having yellow flowers and fruits that dry tan, whereas, *B. alba* has white flowers and fruits that dry black. The only other species of *Baptisia* in Alabama to have white flowers is *B. albescens*. It differs by having shorter calyces (4.5–6.5 mm long) and smaller flowers (13–18 mm long) compared to 7–8 mm and 20–25 mm long, respectively, for *B. alba*. The dried fruits of *B. albescens* are yellow-brown. *Baptisia lanceolata* is unique in having a short terminal raceme (2–6 flowers) and 1–2 flowers in the leaf axis.

The only two *Baptisia* taxa with a state and global rank, *B. australis* (G5T2S1) and *B. megacarpa* (G2S2), appear to be in no imminent danger of extirpation. *Baptisia megacarpa* occurs in nine counties in the southern half of the state and is found in several different habitats (dry woods, mixed hardwoods, densely shaded hardwoods, pine woods, clear cuts, stream edges, and roadsides). *Baptisia australis* occurs only on gravel bars and rocky-river banks of the Little Cahaba River in Bibb County but appears to be well protected. In 1996, The Nature Conservancy purchased land to create the Bibb County Glades Preserve, which protects the section of the river where this taxon is known to occur. Additionally, in 2003, the U.S. Fish and Wildlife Service purchased land adjacent to Bibb County Glades Preserve and created the Cahaba River National Wildlife Refuge. The Nature Conservancy and the U.S. Fish and Wildlife Service both are continuing efforts to expand the refuge, and *B. australis*, along with several other rare taxa, should be protected for future generations.

Baptisia perfoliata, although it has no state or global rank, is the rarest *Baptisia* in the state. It is known from only Sumter County in Alabama, which is the westernmost county in the state. The closest population is Laurens County, Georgia, some 500 km to the east. In 2013, this population consisted of approximately 30 plants. The taxon occurs on land owned by American Legion and is

not considered native to Alabama. It is thought to have been introduced in the 1950's when Auburn University planted longleaf pine brought from Georgia.

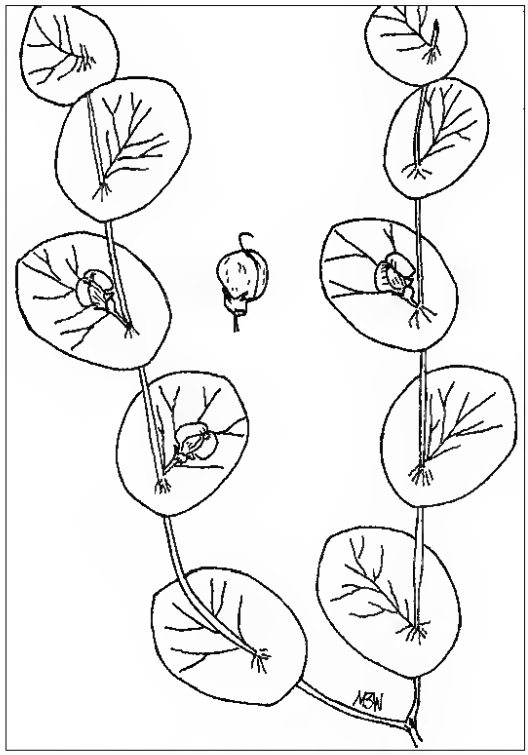


Figure 1. *Baptisia perfoliata*, distribution

Figure 2. *Baptisia australis*, distribution.

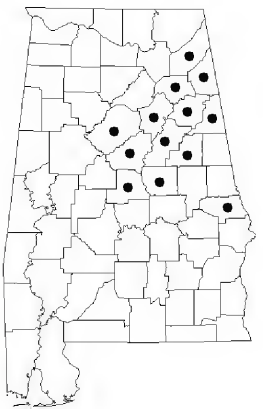
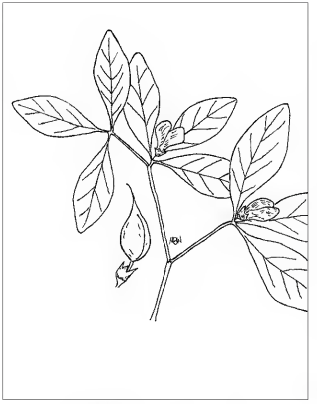


Figure 3. *Baptisia bracteata*, distribution.



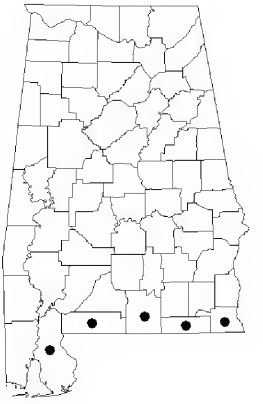
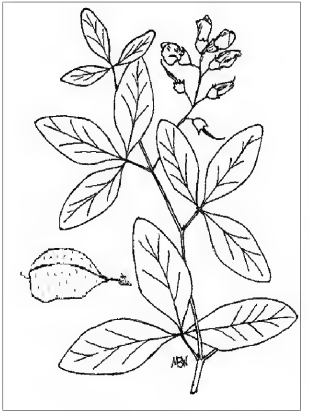


Figure 4. *Baptisia lanceolata*, distribution.



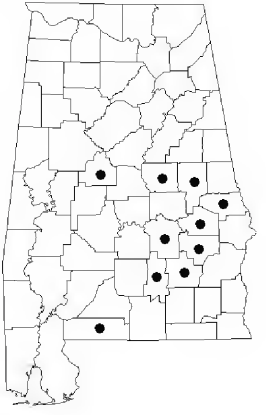
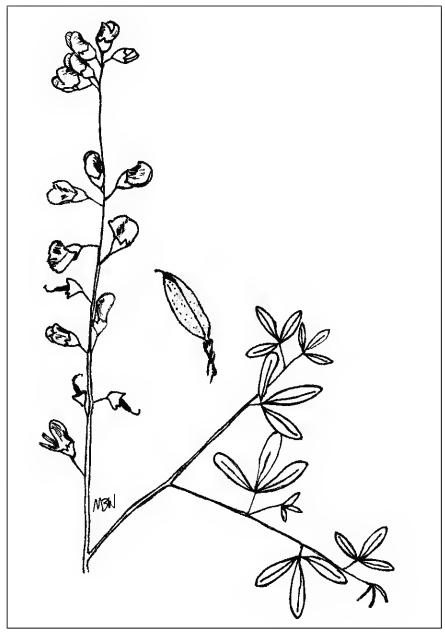


Figure 5. *Baptisia megacarpa*, distribution.



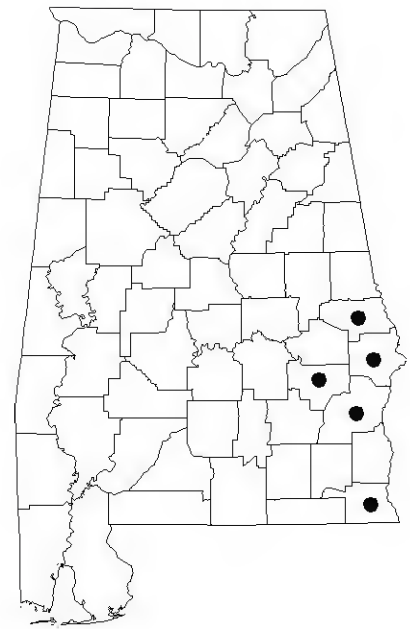


Figure 6. *Baptisia albescens*, distribution.

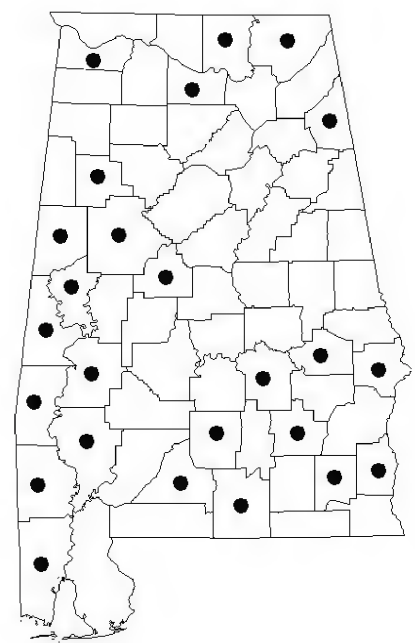


Figure 7. *Baptisia alba*, distribution.

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REVIEW OF CLAIMS OF SPECIES LOSS IN THE FLORA OF CONCORD, MASSACHUSETTS, ATTRIBUTED TO CLIMATE CHANGE

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ABSTRACT

The observations of a previous article (Angelo 2014a) that examined the issue of claimed species loss in the Orchidaceae and Liliaceae of Concord, Massachusetts, are here significantly extended. A comprehensive and detailed review is made of all 192 species claimed to have experienced significant decline in frequency of occurrence in Concord and that were used to determine phenological and phylogenetic correlations in the climate change work of Willis et al. (2008). In addition, I evaluate the methodology and the historical data used by Primack et al. (2009) to determine the species that experienced significant loss and their degree of loss (used by Willis et al.). The recent and comprehensive information used here to make the analysis and evaluation are my recently completed online flora of Concord, Massachusetts (Angelo 2014b), the study of the flora of Middlesex Fells Reservation, Massachusetts (Hamlin et al. 2012), the vascular flora of Worcester County, Massachusetts (Bertin & Rawinski 2012), and the subsequent analysis of the Worcester County native vascular flora by Bertin (2013). The analysis here reveals that only 44 of the 429 Concord species from the Primack et al. (2009) study that are used by Willis et al. (2008) can be claimed with reasonable probability as significantly declining (or to have declined) in frequency of occurrence. Of these 44 species, 24 can be associated with causes for decline other than climate change. Moreover, it is demonstrated that the methodology of Primack et al. (2009) is seriously flawed, that the historical data used for that study are unreliable for the purposes to which they are put, and that the present-day data obtained in that study for uncommon species are also unreliable. Consequently, the dramatic claims by Primack et al. (2009) regarding disappearance of plant species in Concord are unwarranted and the findings in Willis et al. (2008) based upon those claimed disappearances are flawed and unusable.

Primack et al. (2009) surveyed a portion of the flora of Concord, Middlesex County, Massachusetts, between 2003 and 2007, focusing primarily on the protected land of the town. Their findings of species diversity and abundance were compared with the report by Hosmer (1903) for the same general vicinity about 100 years previously. Primack et al. (2009) claim that 24% of 479 native and non-native species seen by Hosmer (1903) could no longer be found and that the losses appeared to be have been sustained mostly in the prior 30-40 years. Willis et al. (2008) utilized data of 429 species from the study of Primack et al. (2008) and phenology data past and present compiled by Miller-Rushing & Primack (2008) to discover correlations between species decline in frequency and historical shifts in average flowering dates. The study found a correlation for species with smaller shifts in flowering dates (comparing recent times and periods in the 19th century) with an apparent decline in frequency of occurrence. In turn such species were found to occur mostly within certain families. The inference drawn was that climate change was responsible for their decline since species that are least able to shift their flowering time due to increasing temperatures are less successful.

In the present study, the methodology and frequency of occurrence data (historical and current) used by Primack et al. (2009) will first be evaluated. Then the group of 192 Concord species (out of 429 species used by Willis et al. 2008) determined by Primack et al. (2009) to have experienced more

than minimal decline in frequency (from 1903 to ca. 2007) will be analyzed using recent information. If the data for changes in frequency of occurrence provided by Primack et al. (2009) are found to be significantly incorrect or unreliable, then the correlations found by Willis et al. (2008) are invalid. Correlations based on the use of faulty data do not confer validity on those data.

Methodology of Primack et. al. (2009)

The concept behind the methodology of Primack et al. (2009) for the species used by Willis et al. (2008) is simple: for each species listed by Hosmer (1903) compare the frequency of occurrence stated by Hosmer (1903) with the frequency of occurrence of the same species in the period 2003-2007. However, multiple, significant problems that are not addressed or disclosed in Primack et al. (2009) are detailed below.

1. Mismatch of study areas

Hosmer's (1903) study area is more than Concord. There is a great difference in the geographical sample area of Hosmer (1903) and Primack et al. (2009). This is clear from the very title of Hosmer's manuscript containing his information. The title is "List of the Wild Flowers (and time of blooming) of Concord, Mass. and vicinity as observed by Alfred W. Hosmer." Hosmer's data include the entire Concord vicinity, not just Concord proper. When Hosmer cites specific locations for species in his list, locations from other townships are included but not typically stated as such. In fact, review of Primack et al.'s (2009) use of Hosmer's records shows that some of those locations (such as Grassy Pond and Stow Swamp) were misconstrued by Primack et al. (2009) to be in Concord instead of in townships outside of Concord, so that the frequency of occurrence assigned to Hosmer's information was increased. These instances are noted in Appendix A below. More importantly, Hosmer's designation of "Common" is not specifically applied only to the plants of Concord but to the Concord vicinity, which includes Lincoln, Bedford, Carlisle, Acton, Sudbury and even non-contiguous Stow (from Hosmer's references to a notable swamp there). One might assert that this is a distinction without a difference, but this is not the case as shown below.

In Willis & Davis (2014) it is implied that, because declines were similarly found when comparing the Primack et al. (2009) survey with data from Henry Thoreau's Journal (1906, all other references to "Journal" are to this) and from Eaton (1974), the much larger Hosmer (1903) sampling area does not significantly change the conclusions. Thoreau in his Journal, however, does not present frequency of occurrence data explicitly, so that such a comparison is not feasible. The frequency of occurrence can be determined crudely in many cases (common vs. uncommon), but only by carefully checking Thoreau's Journal entries for each species, not just using the number of Journal entries for each species. This is due to Thoreau's repeated references to single stations, references to stations outside of Concord, and a great many references that do not cite a specific location. Of the 770 vascular plant species that Thoreau reported or collected in Concord that have been vouchered as occurring in Concord, the frequency of occurrence cannot be even approximately determined for 262 of them, a high percentage. Comparison with Eaton's (1974) information would be a different study and still suffer from the inadequacies identified below.

Plant species are not evenly distributed within the varied habitats of the Concord vicinity, just as the species are not evenly distributed within Concord proper, as the evidence presented below will demonstrate. Striking differences in frequency information occur between Pratt (1878), who limited his work to Concord (with rare exceptions), and that of Hosmer (1903). The difference in sampling areas is the only way to account for these differences. There are even seven instances in just the 192 species reviewed in detail in this article where Pratt (1878) described a species as rare while Hosmer (1903) described it as common, and only two of those seven are alien species (for which a sudden increase would not be unusual). A comparison of all 335 species listed by both Pratt (1878) and Hosmer

(1903) where frequency information is stated or can be determined as either common (including abundant, very common, rather common, common, frequent, and not uncommon) or uncommon (infrequent, uncommon, occasional, scarce, rare) shows that there are 57 instances where Pratt (1878) indicates the species to be uncommon while Hosmer (1903), for the Concord vicinity, indicates the species to be common. In addition there are 36 species not even listed by Pratt (1878) for Concord that are indicated as common by Hosmer (1903), and another 68 species not listed by Pratt (1878) that are described by Hosmer (1903) as uncommon. By contrast, only 17 species are indicated as common by Pratt (1878) and uncommon by Hosmer (1903). So, unless we want to conclude that there was an explosion in abundance for 161 species in Concord between 1878 and 1903, it follows that Hosmer's (1903) frequency information is not entirely representative of Concord proper.

The possibility of less sampling of the flora by Pratt (1878) than by Hosmer (1903) is highly unlikely given that Minot Pratt botanized in Concord for 36 years (1842-1878) while Alfred Hosmer botanized primarily only for 15 years (1888-1903). A familiarity with Pratt's manuscript (1878) reveals that he found a significant number of locations for rare or uncommon plants not found by Thoreau or Alfred Hosmer, each of whom botanized for shorter periods of time. Pratt (1878) lists 587 species in Concord that are vouchered as occurring in Concord (not including 114 species introduced by Minot Pratt himself into Concord) while Hosmer (1903) lists 664 species vouchered as occurring in Concord, including about 10 vouchered Minot Pratt introductions that survived. The main difference between Pratt's and Hosmer's numbers is the advent of new alien species, but some difference also is attributable to the recognition of more species in Hosmer's time that previously were lumped together in Pratt's time. Hosmer's (1903) much larger sample area produces frequencies of occurrence that differ significantly from Concord proper, with many more species found as "common."

Primack et al.'s (2009) study area is less than all of Concord. It is a fundamental principle of measuring population changes to compare the same sample areas. Comparison of the Hosmer (1903) information for the greater Concord vicinity with the much smaller sample area of Primack et al. (2009), focused on the protected areas portion of Concord, would be expected to yield even more incomparable results. This very large differential between sample areas renders invalid the claimed abundance changes of Primack et al. (2009) that were used by Willis et al. (2008).

Primack et al. (2009) purport to measure the effectiveness of conservation efforts by measuring changes in the flora of protected areas of Concord but at the same time announce significant losses for the whole of Concord. There are significant problems with this agenda, the first being that the flora of the protected areas of Concord, as significant as these might be in terms of acreage, is not the flora of the whole of Concord. Numerous stations of uncommon plants are on private, unprotected land, such as in the large sphagnum bog in the southwestern corner of the town, the greater part of Conantum, Ball's Hill, large parts of Punkatasset Hill, an open, sandy plain rapidly disappearing near Second Division Brook, a large part of Fair Haven Hill, Annursnack Hill, and more. The study notes that 35% of the area of the town is actually protected while another 27% is not actually protected but undeveloped and "targeted for conservation efforts." There is no evidence to establish that the flora of the "protected" and "targeted" areas is representative of the flora of the entire town. To measure changes in the protected areas, even including the 'targeted" areas" would presume the capability of identifying what was in those areas compared to the historic time of Henry Thoreau or Alfred Hosmer. The historic information for such a comparison is simply unavailable. Pratt (1878) and Hosmer (1903) only occasionally provided plant locations, some of which are not locatable or are located with great difficulty. Thoreau's Journal is also of little assistance since in a great many instances he provided no location for a given plant find or he used his own place name, which in many cases has yet to be determined in terms of modern geographic coordinates. For Primack et al. (2009) to state that 27% of plants seen by Thoreau were not located is not at all surprising in light of the above considerations

(assuming that their count of what Thoreau saw is accurate). For that study further to claim that 36% of the plant species seen by Thoreau persist currently in only one or two populations "vulnerable to extinction" is to conflate the limited exploration and adequacy of that study to what is actually happening to those species in the entire town. The issue of failure to find plant populations is discussed in more detail below.

2. Differing concepts of frequency of occurrence terms

There is an issue with comparing common English terms for frequency of occurrence between two different observers, particularly ones of different eras. This is acknowledged by Primack et al. (2009), but the number of species affected is claimed to be "probably small in comparison to the total number of species in the study" without any justification, particularly with respect to the subset of species for which significant decline is claimed. There is no evidence to indicate exactly what qualified as "common" or "uncommon" in the mind of Alfred Hosmer. Eight stations of a given species spread over seven townships of the Concord vicinity with only one station in Concord proper might qualify as "common" for Hosmer (1903) but would be "rare" for Primack et al. (2009). Or, a species that occurs in abundance in three townships of the Concord vicinity but not in Concord itself might qualify as "common" for Hosmer (1903) but would be extinct for Primack et al. (2009). In addition, Hosmer (1903) did not provide information on the quantities of plants found at any given station. One of the frequency terms utilized by Primack et al. (2009) noted below refers to numbers of plants at a single station. The problem applies even for Eaton (1974), where the sample area is Concord proper. The terms are nowhere defined quantitatively other than by Primack et al. (2009) for their survey, where "common" was defined as three or more populations, "uncommon" as one or two populations, and this latter category subdivided into "infrequent" for two populations, "rare" for one population with more than 10 plants, and "very rare" for one population with 2-10 plants. It was observed when reviewing the source information for Primack et al. (2009) that when Hosmer (1903) simply listed locations rather than provide a frequency description, the definitions that Primack et al. (2009) used for their own finds were applied to these instances in (Hosmer 1903) to yield values of "common" where Hosmer himself did not apply that term. Thus, there were more instances of "common" for Alfred Hosmer's species than he himself acknowledged.

The increased use of "common" by Hosmer (1903) can be seen statistically. The work of Hosmer (1903) uses "common" in the broad sense (abundant, very common, common, not uncommon) for 61% of the vouchered Concord species (406 out of 664) for which he gives frequency information (and applying the definition of "common" used by Primack et al. 2009). Thoreau's Journal and herbarium yield 46% (218 out of 478 species) for those vouchered Concord species for which frequency can be reasonably determined, excluding grass-like families not treated by Hosmer (1903) or Pratt (1878). The percentage for Pratt (1878) is 52% (310 out of 587 species), and 49% (443 out of 911 species) for Eaton (1974). The generous use of "common" by Hosmer (1903) together with the added application of this term to additional Hosmer (1903) species where Hosmer (1903) did not use it yields an increased appearance of species decline when Primack et al. (2009) fail to find sufficient populations. Furthermore, small differences in occurrence yield the appearance of larger declines using the definitions of Primack et al. (2009). Under the Primack et al. (2009) concept of frequency, failing to find just three more stations of a species where only one station had been found is the difference between "common" and "rare." From the above considerations it should be apparent that the attempt to estimate with any reasonable confidence changes in abundance from Alfred Hosmer's or Thoreau's time by comparing current estimates to Hosmer's (1903) information or Thoreau's very imprecise Journal information is simply not feasible, except for those species that were and are very common and for those that were and have always remained rather rare.

3. Differing experiences of a flora by different botanists, even in the same era

Primack et al. (2009) fail to recognize that different past botanists, skilled and assiduous as they might have been, experienced the same flora differently, ofttimes much differently, such that different evaluations of frequency are reported even for cases where populations of a species haven't changed. For example, in the span of less than a year, with no more than five years of experience in botany, I located three well-separated, healthy populations of *Rhododendron groenlandicum* in Concord. Yet Thoreau, Alfred Hosmer, and Richard Eaton knew it from only the same solitary location in Concord (a location ruined before my time in Concord) and Minot Pratt knew it from only two locations. *Rhododendron groenlandicum* is not an inconspicuous plant and in Concord is close to the southeastern limit of its range, being typically much more common in northern New England. Thus, unless this species somehow tripled in number of stations between the time of Alfred Hosmer and the late 1970s (contrary to the view that northern species are retreating northward due to climate warming), one can confidently presume that there were at least four stations of this native shrub in Concord in the time of Thoreau. The varying frequencies attributed to the various Concord botanists for this species according to Primack et al. (2009) would have been rare, infrequent, and common. Primack et al. (2009) found none of the locations, so that "extinct" would be added to this list. Given the great variance in finding this species by past botanists, the confidence level of a report of its extinction should be low. *Rhododendron groenlandicum* is not an isolated example. In my previous article (Angelo 2014a) I noted much the same results for *Phegopteris connectilis*, and there are other similar examples cited in Appendix A below.

To give a quantitative measure of this, it is revealing to compare the experiences of Thoreau and Minot Pratt, who both botanized in Concord at about the same time and were friends. There are about 374 species vouchered to occur in Concord for which it is possible to discern from Thoreau's Journal whether he found them common or uncommon in Concord and for which Pratt (1878) also provided frequency information. Of these are 58 for which Thoreau did not find the species common while Pratt (1878) found them common. There are 18 species for which Thoreau found the species common but Pratt (1878) did not found them common. Thus, there was disagreement for 76 of 374 species, or 20%. The conclusion should be that any finding that there are many stations of a species in a survey of a given, sizable area is relatively reliable (barring issues of difficulty in identification). Also, findings of relatively few stations of a species are subject to a large margin of error, unless the habitat for the species is known to be rare in the study area (such as sphagnum bogs or serpentine outcrops). Primack et al. (2014) make the point that multiple botanists, including myself, were consulted to ensure an accurate inventory of Concord's flora. But I (and other local botanists) did not make an attempt to correct all the failures to find plants of Primack et al. (2009). I merely provided information on where a limited number of uncommon plants had been found by me in the past. Also, local botanists do not carry in their memory or notes the locations of all occurrences of all common and uncommon species that they have seen over many years of exploration of an area. The amount of time necessary to remedy the notable abundance of failures of Primack et al. (2009) to find species in Concord would be enormous, even if feasible, as discussed below (7. Insulation from falsifiability).

4. Significance of population size

Primack et al. (2009) attach undue significance to numbers of individuals for a given station of a species. Their study defines a separate category of "very rare" for single stations with 10 or fewer plants. This is an arbitrary number. While the number of plants at a lone surviving station in a large area is relevant for the survival of that species in that area, some species are naturally distributed in small quantities in scattered stations. When one of the authors of (Primack et al. 2009) was shown stations of species in Concord at the time of their study that those authors claimed to be "lost" (simply because they failed to locate them), the demonstrations of continued existence of those species in Concord were typically dismissed as insignificant based on the small number of the plants at the station

and upon the fact that more stations were not at once demonstrated. Experienced field botanists know that finding a single population of a species with few individuals does not signify that one has by remarkable chance found the last, dying group of the species in the entire area, regardless of how many hours might have been spent wandering the woodlands, swamps, etc., on the look-out for it. Instead, it is virtually always a sign that there are more populations as small or larger somewhere in the vicinity that have yet to be found. Some species simply do not inhabit the environment in large populations as do *Maianthemum canadense* or *Gaylussacia baccata*. Instead, they disperse themselves in small, sometimes widely separated groups that have long thrived in that mode of distribution.

For example, Pratt (1878) noted for *Asclepias amplexicaulis* that it was sparingly scattered in all quarters of Concord, while Thoreau did not notice it in Concord until 1852, about 10 years before his death. In my time in Concord in the 1970s/80s I observed this same sparse distribution pattern. In 2007 on a brief visit to Concord I found a modest amount of this plant along a road where I had seen it about 30 years before. Upon directing one of the authors of the Primack et al. (2009) paper to this location (since in the 4-5 years of that study they had found none) this station was dismissed at once as insignificant due to the smallness of the population (about 20 plants). This reflects an ignorance of the ecological and historical context of this species in Concord. It is likewise with *Asclepias exaltata* for which Pratt (1878) noted its occurrence only in the northerly part of the town and that there were not more than three or four plants in all. I found *A. exaltata* in my time in Concord at six locations, but never with more than a few plants at each location. *Asclepias amplexicaulis* and *Asclepias exaltata*, unlike their vigorously vegetatively reproducing sister species, *Asclepias syriaca*, never occur in Concord in great quantities, illustrating clearly that species in Concord within the same genus can march to different drummers. Failure to recognize this ecological fact and the reproductive nature of individual species is to misread the Concord flora, or any flora, such as at Middlesex Fells. While increase or decrease in numbers of a particular population at a particular site might be of interest, we simply do not have that level of detailed information from past botanists in Concord for a significant spectrum of the flora. The peculiar view adopted by Primack et al. (2014) is that happening to find one population with a relatively small number of individuals invariably portends the extinction of the species in the near future, a view that is without foundation. New stations for a species, for instance, will start small. If the view is simply that it is more likely to become extinct, this too is unsubstantiated, particularly given the fact that all stations of the plant are not known. If a species is known with certainty, due usually to rarity of habitat, to occur only in few numbers at a very few sites, then those would, of course, be more vulnerable to extinction. But the key point is knowing with certainty how many stations there really are and the natural distribution pattern for the species.

5. Inadequacy of exploration — under-sampling

This is might be the most significant problem with the study by Primack et al. (2009). That study does not take into account the possibility of inadequacy of their survey for the variety of reasons identified in my previous article (lack of access, lack of skill at locating particular species, limited exploration). Primack et al. (2009) were unable to find 70 of Hosmer's (1903) 322 native Concord species used by Willis et al. (2008), including *Myrica gale*, *Clintonia borealis*, and *Andromeda polifolia*, known to be currently in the town. Earlier indications of inadequate sampling are found in Drayton & Primack (1996) where, for example, among the species claimed as "lost" were the showy, wetland species, *Lobelia cardinalis*, *Ilex verticillata*, and *Lysimachia terrestris*, all of which Hamlin et al. (2012) found to be common and not at all "lost" or hard to find. One of the clearest signs that the study by Primack et al. (2009) has significantly underreported the occurrence of species in Concord is the reporting of some currently common, easy-to-recognize, native species as "infrequent" (only two stations) in Concord. These include *Mitchella repens* (currently plentiful and common throughout Concord), *Houstonia caerulea* (more than seven locations, several of these in abundance), *Sassafras albidum* (currently more than 12 stations) *Anemone quinquefolia* (abundant with many more than four

stations), *Chimaphila umbellata* (more than four stations), *Gaultheria procumbens* (plentiful with many more than four stations), *Apios americana* (plentiful with many more than four stations), *Lobelia inflata* (plentiful with many stations), and *Sium suave* (plentiful with many more than four stations), as reported by Cherrie Corey (2014 pers. comm.) and Cole Winstanley (2014 pers. comm.). See Appendix A for details for some of these. All of these but one are currently common in both Worcester County (Bertin pers. comm.) and at Middlesex Fells (Hamlin et al. 2012). That one, *Houstonia caerulea* (not common at Middlesex Fells), however, is widespread and abundant in Concord as noted above. For a study of Concord purporting to be intensive (for at least four years) to fail significantly in finding these nine, well-known, common species, corroborated as currently common in studies of locales near Concord as well as by local Concord resident naturalists, implies that the findings of the Primack et al. (2009) study for other common species and especially uncommon species cannot be relied upon.

It is not for this article to determine the reasons for the failure just noted. The limitation of Primack et al. (2009) in their explorations of Concord primarily to "protected areas" could be a contributing factor, although the finds of Cherrie Corey and Cole Winstanley noted above are mostly on protected lands. Even in exploring such areas there is no means available to evaluate how thorough the authors were in exploring those areas. Lack of access to important privately owned tracts of land might also be a factor. The skill of the authors of the Primack et al. (2009) study in recognizing and finding plants could be a major factor.

Additional indication of underreporting of species abundance by Primack et al. (2009) is the fact that 57 of 171 species (adjusted from 192 to remove unusable taxa as detailed below) claimed by that study to have significantly declined in abundance have not declined or are only minimally declined in frequency in the recent studies of Worcester County (Bertin & Rawinski 2012) and the Middlesex Fells Reservation (Hamlin et al. 2012), as detailed in the Appendix A. The finding of Primack et al. (2009) that significant numbers of species declined only between the time of Eaton (1974) and Primack et al. (2009) rather than between older botanical surveys is not at all surprising if the Primack et. al. (2009) findings are significantly inadequate, as is indicated above. Also, the finding of Primack et al. (2009) that species reported by Eaton (1974) as uncommon to one degree or another were the ones mostly found by them to have become "locally extinct" is consistent with the greater likelihood that their inadequate survey would be less likely to find uncommon species (since they even had difficulty finding species that have remained common through time).

Primack et al. (2014) make the argument that a comparison is not feasible between two floral studies of a given area, as between Drayton & Primack (1996) and Hamlin et al. (2012), or between the latter and Deane (1896), because comparable numbers of investigators did not spend comparable numbers of hours. This assumes not only that effectiveness of study is directly proportional to hours spent between different individuals but also that Primack et al. (2014) have accurate information on the number of hours spent by Hosmer (1903) botanizing in Concord proper and on the number of hours expended by those botanists known to have provided the information used by Deane (1896). Even with this knowledge, the point of Primack et al. (2014) renders comparison between all studies unreliable (including between Hosmer 1903 and Primack et al. 2009), as no two of them will have spent comparable time, assuming such time is equally effective. Thus, the findings of thorough multiple studies over time and in neighboring areas is essentially the only way to obtain a reasonable understanding of what changes are actually occurring for each species.

6. Alien species

The inclusion of alien species in presenting claims of species loss is questionable. The disappearance of alien species in any area has much more to do with changes in cultivation practices (agricultural, ornamental, seeding projects) and industry (presence or absence of textile mills, extent of railroads, etc.) than it does with broader environmental changes. This can be seen in the species-by-species review of the 192 species (native and alien) of claimed significant decline used by Willis et al. (2008). The case of *ASPARAGUS OFFICINALIS* is particularly dramatic with the frequency of occurrence tracking clearly the great expansion of asparagus farming in Concord right after the time of Thoreau followed by the significant decrease in this farming in the 20th century. Bertin and Parise (2014) appropriately analyze abundance changes of non-native species in Worcester County, Massachusetts separately from native species (Bertin 2013).

With regard to discerning effects of climate change, including alien species is unwarranted and misleading. Such species have not adapted to the local environment over hundreds or thousands of years as native species have. The fact that they can be introduced into and multiply so quickly in Concord demonstrates that they are sensitive to factors that do not affect the native species correspondingly. These species by their nature tend to be very adaptable to new environments and changes in the environment. Jonathan Lenoir, lead author of a study cited by Willis et al. (2008), has expressed agreement (2014 pers. comm.) with this, stating "for non-native plants it is very hard to disentangle the pure effect of climate warming from the niche-filling effect of the alien in its non-native range after human introduction." Bertin & Parise (2014) have concluded that their study provides "some of the strongest quantitative evidence of the important link between human modification of the landscape and the success of nonnative plant species for any region of North America." and that "Residential land use is a key correlate of the occurrence of nonnative species." Bertin and Parise (2014) considered a variety of factors that could account for the patterns of increase and decrease of nonnative species without finding climate change as a key factor. Among the 429 species used by Willis et al. (2008), 107 were nonnative species, predominantly from Eurasia, of which only 102 are actually usable (see discussion below). Of these 102 nonnative species, 38 species were claimed to be declining in the data used by Willis et al. (2008) and were used to find correlations of decline attributed to climate change.

Of the 171 species (adjusted from 192 to remove unusable taxa, as explained below) claimed by Primack et al. (2009) to have *significantly* declined in frequency of occurrence in Concord and used by Willis et al. (2008), 27 are alien species, or slightly more than 15%. This is not unusually high, but it is a significant number. It would be best for studying species decline to limit the study to native species, removing the modest but significant alien component of the species studied. To be sure, it is of interest to monitor changes in nonnative species in the flora (as Bertin and Parise 2014 do), but the results should not be mixed with those of the native species (as do Primack et al. 2009 and Willis et al. 2008).

7. Insulation from falsifiability

The nature of the study of Primack et al. (2009) is such that, for practical purposes, it is not possible to prove definitively that the claims of significant species loss are either false or significantly in error. Consider what it would require to change significantly the finding of loss for just one species. Suppose that Hosmer (1903) claimed that a particular Concord species was frequent and that Primack et al. (2009) were unable to find any stations for the species. First, it is not possible to prove that Hosmer (1903) was in error or to what degree, other than by indirect means as reasoned earlier, but which Primack et al. (2009) can simply choose not to accept. Secondly, to prove that the failure to find the species in the modern era was significantly in error would require spending time and effort to search a large area for a species that is possibly uncommon, in order to locate two or three stations. Even if

that effort were successful, the authors are likely to dismiss the stations as insignificant if a sufficient number of individuals is not found at each station or if there is only sparse flowering among the individuals found (as one of those authors has been done). Lastly, even if the authors accept the fact that they are in error for that one species, the argument will be that the results of their study are unaffected since the remainder of the many losses claimed still have not been disproven. In effect to prove the study significantly in error the entire study would need to be redone. This effectively insulates the findings of that study from falsifiability for practical purposes, other than by a combination of direct and indirect means as is done here. A case where such a study was redone was for Middlesex Fells, in which one of the authors of Primack et al. (2009) was also involved in the original study there. The redone study (Hamlin et al. 2012) did in fact find the results of the earlier study (Drayton & Primack 1996) to be significantly in error with respect to the current state of the flora. Even so, Primack et al. (2014) have attempted to argue that those recent findings do not change the claims of losses in their original study in Drayton and Primack (1996).

Review of the 192 Concord species claimed to have significantly declined by Primack et al. (2009) and used by Willis et al. (2008)

A means is used here to conduct a check on the Concord species declines reported by Primack et al. (2009) and used by Willis et al. (2008) in a manner that avoids the insulation-from- falsifiability barrier of the former study (discussed above). The 192 species among the 429 Concord species used by Willis et al. (2008) showing more than minimal decline were considered one by one in their ecological, historical and regional context: first, to determine if they were actually listed by Hosmer (1903), free of taxonomic issues, and possessing usable frequency of occurrence information by Hosmer (1903); second, to determine if there truly is a decline and to what degree; and third, to determine whether or not any possible or likely decline might be related to climate change (avoiding decline linked to other causes or decline that is only local). By removing species whose decline cannot be measured and those for which any decline would not be related to climate change, a residue of species suitable for investigation is obtained. The number of these is much less than the 192 species of claimed significant decline used by Willis et al. (2008). Species of minimal decline (a decrease of only -1 using the method of Willis et al. 2008 as explained below) are not considered here, as the margin of error (for actual decline) is too significant, either on the Hosmer (1903) or Primack et al. (2009) side or both. There were 92 such species of claimed minimal decline that were not reviewed one by one. To demonstrate the unlikelihood that consideration of these would likely yield many additional species worthy of consideration, a check was made to see how many of these are reported as currently "common" in both Worcester County (using Bertin & Rawinski 2012) and in the Middlesex Fells Reservation (Hamlin et al. 2012). It was found that there were 48 species meeting these conditions alone. Applying the other checks (taxonomic, observations of current frequency, other causes, etc., as are applied to the 192 species with significant decline) on the remaining 44 species of minimal decline (including 8 nonnative species) would most likely reduce these to relatively few, if any, and, in any case, would be of minimal significance. They would be of minimal significance since minimal decline as used by Willis et al. (2008) is essentially the difference in finding only one less station for a species currently than historically — easily within the margin for error.

1. Assumptions of Willis et al. (2008)

Willis et al. (2008) attempt to link correlations of Concord species declines as determined by Primack et al. (2009) with the lack of responsiveness in flowering times in some species to changes in average temperature in the environment (phenologically challenged species). The phenologically challenged species were in turn phylogenetically correlated (suggesting phylogenetic conservatism for this shared trait). Finding such correlations suggests the operation of climate change in species declines. This attempt is not possible if the underlying species losses claimed are not real or are not reliable. If the species losses are not distributed as claimed or not as pronounced as claimed, then any

correlation found is not significant. The attempt is also not credible if many species losses can be determined with reasonable likelihood to be attributable to causes other than climate change and/or to have occurred before climate change is likely to have been significant. For reference, the set of 429 Concord species used by Willis et al (2008) is listed in Appendix B along with the degree of change in frequency of occurrence for each species used in that study which was derived (as explained below) from Primack et al. (2009). Of the 429 species used by Willis et al. (2008), 265 species (62%) are in the families noted in that study as implicated phylogenetically for having phenologically challenged constituents. Thus, if Primack et al. (2009) were generally inadequate in finding plant species, then species declines are overreported and those purported declines would more likely show up in these families, giving the appearance of a correlation of losses with families having more phenologically challenged species.

Willis et al. (2008) assigned number values not only to the frequency of occurrence in Concord claimed by Primack et al. (2009) but also to the frequency of occurrence in the greater Concord vicinity reported by Hosmer (1903). This implies a degree of accuracy in the reports of Hosmer (1903) and Primack et al. (2009) that is neither warranted nor justifiable. As discussed and illustrated above, neither of these two sources is particularly reliable. The work of Hosmer (1903) tended to find more species as "common" than did Pratt (1878) before him and Eaton (1974) after him. Of the 402 Concord species (not just those used by Willis et al. 2008) reported on by all three of these botanists, Hosmer (1903) reported 316 species as common or frequent, Pratt (1878) reported 276 species, and Eaton (1974) reported 257 species. This parallels a similar comparison made earlier. The near agreement between Pratt (1878) and Eaton (1974) with fewer common species reported by Eaton would be expected. The excessive use of "common' by Hosmer (1903) is in accord with the discussion above — Hosmer's much larger sample area and perhaps more generous concept of "common." Thus, there is a built-in bias toward "common" in the Hosmer (1903) data.

Willis et. al. (2008) assigned to Hosmer's (1903) and Primack et al. 's (2009) frequency information the number values 6 for "very common," 5 for "common," 4 for "frequent," 3 for "infrequent," 2 for "rare," 1 for "very rare," and 0 for absent in the flora, where "very common" means found throughout the area, "common" defined as more than three stations, "frequent" as three stations, "infrequent" as two stations, "rare" as one station with more than ten plants, and "very rare' as one station with ten or fewer plants. By creating two categories for rare occurrence in effect magnifies the amount of decline for species that cannot be located at all. The assignment of such quantitative measures to the approximate qualitative terms of Hosmer (1903) is artificial and unrealistic given the considerable variation in evaluating frequency of occurrence not only between different botanists but also from species to species. As noted above and in my previous article (Angelo 2014a), no one botanist or small group of investigators can assess the frequency of occurrence of any given species with the accuracy presumed (allowing for some inaccuracy) by Willis et al. (2008), particularly for those species that are not common or occur in small numbers at each station. It was noted above that Primack et al. (2009) even had difficulty correctly assessing the frequency for common species. With the inapplicability of and overreporting of "common" in the Hosmer (1903) information combined with the undersampling of the Concord flora by Primack et al. (2009) compared to previous Concord botanists, it is understandable that significant declines were reported by Primack et al. (2009). The assumption built-in to the study of Willis et al. (2008) is that the approximate estimates of Hosmer's (1903) frequency of occurrence of species in the Concord vicinity are sufficiently accurate measurements for Concord proper and that the findings or lack of findings of Primack et al. (2009) are also sufficiently accurate.

An assumption by Willis et al. (2008) is that an apparent strong correlation of species declines in those plant groups containing phenologically challenged species likely means that declines in these groups are related to climate change. Simply because correlations with other measurable factors are

not found does not automatically mean that other factors are not operating in any decline, as is acknowledged by Willis et al. (2014). Multiple other factors (habitat destruction/degradation, local water pollution, competition from new alien species) accounting for significant decline in different groups operating in different degrees would lessen or even alter the apparent correlation found for phenologically challenged species. A reasonable description of some of these other factors was given by Primack et al. (2009), to account for the losses they claimed, without assigning primary cause to climate change. A far more extensive and detailed discussion of multiple causes of abundance changes is given by Bertin (2013) in his analysis of changes in the native flora of Worcester County, Massachusetts. While it was found by Bertin (2013) that northern native species declined relative to southern species, as would be expected due to warming average temperatures, this was only one of multiple other likely or possible causes of frequency of occurrence changes. Declines were found by Bertin (2013) to be significant in a much smaller number of taxonomic groups than claimed by Willis et al. (2009), even though Bertin (2013) studied the entire flora of the study area, unlike Willis et al. (2008). Moreover, declines in some of these groups noted by Bertin (2103), such as in *Ribes* and *Crataegus*, can be understood to be due to causes other than phenology or climate change. The correlation detected in Willis et al. (2008) should not blind one to the effects of other causes or to dismiss those other causes as insufficiently significant when in fact they can be the more important cause of most declines.

2. Timeline of climate change effects

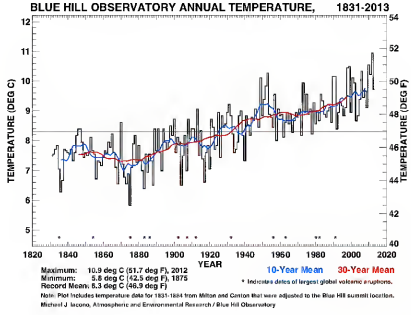
If climate warming is causing some species to decline in frequency of occurrence, there are questions as to the magnitude of warming necessary to create an observable effect, how much decline ensues for a given amount of warming, how rapidly the effect occurs, and over what historical periods would this effect be expected to be detectable. For the most part the answers to these questions are not known, at least definitively. It is reasonable to assume that warming would affect different species variably in a more or less continuous spectrum of sensitivities.

Three studies are cited by Willis et al. (2008) to support the effect of climate change on plant species occurrence. One (Sturm et al. 2001) shows that shrub abundance increased in the Arctic between ca. 1949 to 2000, which is to be expected at the northern range limit of species with climate warming. Another study (Beckage et al. 2008) found that there was a shift in abundance at the margins of the northern hardwood-boreal forest ecotone distributed altitudinally in the Green Mountains of Vermont between 1964 and 2005. Northern hardwoods increased significantly in dominance in the lower portion of the ecotone, while the boreal forest correspondingly declined within this lower portion. This would be equivalent to a northward shift latitudinally at the northern range limit of the more southerly hardwood species, again to be expected with climate warming. The third study (Lenoir et al. 2008) was a large-scale study in France that demonstrated an upward altitudinal shift in the optimum elevation for many forest species for the periods 1905 to 1985 and 1986 to 2005, with the shift being larger for species restricted to mountain habitats and for "grassy" (i.e., herbaceous) species, which are characterized by faster population turnover.

The findings of the above three studies indicate observable effects of climate change in the decades immediately preceding 2005. The findings of the third study suggest that there would be an analogous shift in optimum latitude for plant species such that some native species would increase while others would decrease in frequency of occurrence. The compression of this effect altitudinally compared to latitudinally is likely to make the latter effect more difficult to document. Since more native plant species occur in North America as latitude decreases, a general shift northward in the optimum latitude in the distributions of species should imply that more native species would increase in abundance in Concord than decrease, contrary to the findings of Primack et al. (2009). No attempt was made in this third study (Lenoir et al. 2008) to relate declines in frequency of occurrence to flowering time changes, and no widespread, unexplained declines were reported. Even though increase

in average annual temperature in recent decades has been widely established, the effect on plant populations is by no means consistent. For example, a very recent study of 296 plant species using an extensive network of occurrence records over a 40-year period demonstrated that most (63%) plant species migrated downward in elevation toward increased warmth and precipitation in a climactically diverse section of western North America (Harsch & HilleRisLambers 2014)

To see what changes in average temperatures have occurred in Concord from the time of Thoreau to the present, the most applicable records for the longest period of time would be those of the Blue Hill Observatory in Milton, Massachusetts, 33.3 kilometers (20.7 miles) southeast of Concord. Blue Hill Observatory is the home of the oldest continuous weather record in North America. It is located 17.8 kilometers (11 miles) south-southwest of Boston, while Concord is 25.7 kilometers (16 miles) northwest of Boston. As the Blue Hills Observatory is situated a little closer to Boston than to Concord and in a direction from Boston where there has been dense, urban development, it would be expected that the average temperatures would be moderately higher than in Concord due to the influence of the Boston heat island, especially in the 20th century when this heat island would have developed most significantly. In other words the recorded average temperature increases at the Blue Hill Observatory would be accentuated to some degree compared to Concord. However, for the purposes of this discussion, only the relative increase in mean average over historical periods is of interest, not the absolute increase.



A chart of historic Blue Hill Observatory annual temperatures is given above. From this chart the following can be determined:

Changes in 10 year mean average annual temperature (10YR-AVG) at Blue Hill Observatory, Massachusetts

Period	Starting 10YR-AVG	Ending 10YR-AVG	Change
1878-1903	7.2 C	7.8 C	+0.6 C
1878-1974	7.2 C	8.8 C	+1.6 C
1974-2004	8.8 C	9.4 C	+0.6 C

The dates chosen correspond approximately to the dates of the floras of Pratt (1878) and Hosmer (1903) and the study of Primack et al. (2009).

The comment by Primack et al. (2009) that most of the claimed disappearance of species since Thoreau's time (died 1862) seems to have occurred in the 30 to 40 years prior to that study (1964 to 2004) appears to be at odds with the fact that the increase in 10-year mean average annual temperature at the Blue Hill Observatory from 1878 to 1974 was 1.6 C, while the increase from 1974 to 2004 was only .6 C. From the above numbers one would expect that if climate warming were responsible for significant declines in species, the preponderance of such decline would be expected prior to 1974 and not after it. To test whether in fact there was an apparent significant decline in frequency of occurrence in Concord from 1878 to 1974, it is only necessary to compare the frequency (common vs. uncommon) for native Concord species reported by Pratt (1878) for the same native species as reported by Eaton (1974). There are 416 vouchered native Concord species (including species not used by Willis et al. 2008) where "common" (including frequent, very common, abundant) or "uncommon" (including infrequent, occasional, rare, extinct) is indicated by both Pratt (1878) and Eaton (1974). Of these, 60 native species are reported by Pratt (1878) to be common that Eaton (1974) reports as uncommon, that is, ones that have decreased in frequency. There are 36 native species reported by Pratt (1878) as uncommon, but reported as common by Eaton (1974), that is, ones that have increased in frequency of occurrence. For the remaining 320 native Concord species there was no significant difference in frequency of occurrence reported by Pratt (1878) and Eaton (1974). Thus, there is only a slight margin of net species showing decline (24 out 416 native species). This is not the striking evidence of species declines one would expect for a 1.6 C increase in average annual temperature compared to a 0.6 C increase (for a period where change has been observed), if climate warming was causing significant losses in native species.

A similar comparison can be made between Pratt (1878) and Hosmer (1903), assuming, only for the sake of illustration, that Hosmer's greater study area is sufficiently representative of Concord. There are 355 native species for which Pratt (1878) and Hosmer (1903) both indicate common or uncommon. Of these, only 16 species are reported as common by Pratt (1878) and uncommon by Hosmer (1903). Yet there are 48 native species reported by Pratt (1878) as uncommon but that are reported as common by Hosmer (1903). This would represent a significant net *increase* (32 native species out 352) in species of increasing in abundance from 1878 to 1903 when the 10 year average mean temperature at Blue Hill Observatory *increased* by an .6 C, contrary to the claim of Primack et al. (2009) that there is species decline over time and the claim of Willis et al. (2008) that there is significant decline due to climate change. The more likely explanation is that the Hosmer (1903) frequency data are not representative of Concord proper as noted earlier. To repeat, Minot Pratt botanized in Concord for a much longer period (36 years) than Alfred Hosmer (15 years), and Minot Pratt limited his flora to Concord proper, while Alfred Hosmer did not. In preparing my online flora (Angelo 2014b) it was apparent in comparing Pratt (1878) and Hosmer (1903) that Pratt knew the Concord flora better than Hosmer, finding more locations of rare or uncommon plants that Hosmer (1903) did not find, but that I found in the 1970s/80s.

In light of the preceding, any claim that there was a dramatic decline of species in Concord from 1974 to 2004 is contrary to evidence and would be more indicative of the inadequacy of the survey of Primack et al. (2009) than of a significant decline in that period due to climate change. The evidence used below of recent studies in nearby areas will point to more limited species declines that might be related to climate change.

3. Use of recent studies to discern widespread species decline

If a species has suffered significant decline due to climate change, it would not do so just in Concord, Massachusetts, but also in areas close by. This would be true whether climate change might cause a decline throughout the range of the species or just at the margins of its distribution. It is therefore valuable to have current information from recent, careful studies in Worcester County,

Massachusetts (Bertin & Rawinski 2012; Bertin 2013) and Middlesex Fells Reservation, Massachusetts (Hamlin et al. 2012), to gauge what is actually happening in areas relatively close to Concord. Worcester County is a county in central Massachusetts that is adjacent to Middlesex County, where Concord is located. Its center is approximately at the northeast border of the town of Paxton, which is about 45 kilometers (28 miles) west southwest of Concord. The Middlesex Fells Reservation extends over several towns and cities in Middlesex County, primarily Medford and Stoneham. It is located about 29 kilometers (18 miles) due east of Concord. The location of these two areas bracket Concord geographically very well. The recent floristic studies of these two areas close to and on either side of Concord at approximately the same altitude and latitude offer an excellent opportunity to evaluate what is actually happening in terms of changes of species frequency of occurrence and indications of the reasons for some change.

Worcester County has an area of 3,919 square kilometers (1,513 square miles) with elevations ranging from 48 meters (157 feet) to 611 meters (2006 feet). Like Concord, it has a significant river flora with multiple rivers, including the sources of both the Assabet and Sudbury Rivers, which join in Concord to form the Concord River. The variety of habitats and topography within the county are as varied or more varied than in Concord, including an urban area (city of Worcester). It retains more of the open, dry expanses of land, agricultural lands, and unspoiled sphagnum bogs than does Concord.

The Middlesex Fells Reservation has an area of 10.4 square kilometers (4.0 square miles) with elevations ranging from 19.8 meters (65 feet) to 96.6 meters (317 feet). It has no rivers and no kettle-hole sphagnum bogs, thus lacking, in these respects and perhaps others, the habitat diversity of Concord. It is surrounded by a highly developed urban/suburban environment, being much closer to Boston, but within its borders it presently is relatively protected from further development, unlike Concord.

For comparison, Concord has an area of 67.08 square kilometers (25.9 square miles) with elevations ranging from about 35.4 meters (116 feet) to 110 meters (361 feet). Concord has two rivers that join to form one and has the remnants of several sphagnum bogs. It also has several areas with some calcite and small pockets of limestone in the otherwise acidic soil. While there is significant development in the town, there are many areas that are currently protected from development.

Thus, Concord represents in different ways a transition from the more urban-influenced Middlesex Fells to the less developed Worcester County. The recent flora of Worcester County (Bertin & Rawinski 2012) contains designation of current frequency of occurrence for each species as well as indication of cases where there is decline or increase in a species when compared to records prior to 1980 or in some cases relative to the last historic date of collection. Bertin (2013) analyzed over 67,000 recent observations of native plant species in Worcester County supported by over 6,700 recent herbarium collections and compared them to information obtained from approximately 36,000 historical herbarium specimens. Using that information, each native species was given a change index number between +1.0 and -1.0, where the number represents the difference between the number of townships with post-1980 observations/collections and the number of townships with pre-1980 herbarium records divided by the total number of townships where the species has been recorded. Robert Bertin, the author of the study, has stated that other than for the city of Worcester itself, just about all recent records date from 1998 or later, with the majority from 2003 or later (Bertin pers. comm 2014). Thus, a good record for current status and state of flux is provided by this flora. Likewise, the careful work in the recent Middlesex Fells Reservation by Hamlin et al. (2012) provides the current status (observations of multiple investigators from 2003 to 2011) and compares it with a detailed flora published in 1896 (Deane 1896).

Application of the results of the two recent studies on either side of Concord, combined with direct recent observations of Concord residents and consideration of ecological and historical context, permit a reliable approximation of the status of the 192 species in Concord (adjusted to 171 usable species, as explained below) claimed to be significantly declining. In effect, the review below, using the recent neighboring floristic studies screens out the local effects due to causes of decline particular to Concord or metropolitan Boston or due to the inadequate sampling by Primack et al. (2009).

4. Results and significance

Each plant species has its own story — its own ecological and historical context, its own biological behavior. Before applying a statistical broad-brush to the floral inhabitants or former inhabitants of a local community, it is worthwhile to review to the extent possible, directly or indirectly, what is happening for each species. It is also necessary to consider whether some species should be removed from consideration on other grounds (taxonomic, absence of data, etc.) as explained below. This is to limit consideration to those species that might be responding significantly through their frequency of occurrence to climate change and not more seriously affected by other factors, whether known or unknown. The number of usable species with claimed significant decline is 171 of the 192 such species used by Willis et al. (2008), since 21 species must be removed from consideration based on the problems discussed in the first three categories below.

This species-by-species review of 192 species with claimed significant decline used by Willis et. al. (2008) is given in detail in Appendix A below. As a result of this review the species were placed into one of 11 categories. The categories are reviewed here so that the reasoning for each category can be understood.

1. Not listed by Hosmer (1903) under any name. Four species among the 192 Concord species with significant decline listed in the unpublished spreadsheet provided by Willis are not to be found in Hosmer (1903) under the name in the spreadsheet or under any equivalent older name or synonym. The reason for this is unknown but most likely due to an imperfect attempt to convert one of Hosmer's (1903) names to a modern equivalent. *Lechea tenuifolia*, for example, was a perfectly distinct species in Alfred Hosmer's time and in fact has been documented from Concord. But Hosmer (1903) does not list it, so that it is not possible to derive a change in frequency in this species based on Hosmer (1903).

2. Taxonomic problems. Eight species were found to be listed in Hosmer (1903) using names that at that time comprised what are currently two or more species found in Concord, even though the particular name used by Hosmer (1903) might correspond to a particular modern name. Since a study trying to measure change in frequency must be comparing equivalent taxonomic entities to yield meaningful results, these instances must be removed from consideration. In one case, *MENTHA PIPERITA*, the taxon is now considered to be a hybrid (with non-native parents), so that its biology would make it an unsuitable taxon for a study of change in frequency of occurrence.

3. No frequency information provided by Hosmer (1903). For nine species listed by Hosmer (1903) and used by Willis et al. (2009) and Primack et al. (2009), Hosmer (1903) provided no information whatsoever other than flowering dates, or he provided merely habitat information which Primack et al. (2009) presumed without justification to be a statement of frequency of occurrence — typically interpreted as "common." When Hosmer annotated a species only with "River," "Swamps," "Roadsides," "Brooks," etc., without providing frequency information, frequency for Concord was presumed to be "common" by Primack et al, (2009). For example, "River" could refer to one or more of the towns Concord, Lincoln, Sudbury, Bedford, Carlisle, or even Acton or Maynard without knowing which ones or how many stations there are, or in which towns. As with Pratt (1878), Hosmer

(1903) sometimes chose to list only the habitat of a species without committing to any particular frequency of occurrence. Such instances are not usable to measure frequency of occurrence change.

4. Hosmer (1903) frequency information conflicts with Pratt (1878), and with Thoreau. Primack et al. (2009) stated that "Minot Pratt's observations overlap those of Thoreau and Hosmer, …" If that is in fact the case, then the findings of Pratt (1878) for the most part should not differ greatly from those of Hosmer (1903). Yet in fact, there are 23 species of the 192 species of claimed significant decline for which this is the case. It is not to be expected that between 1878 and 1903 there would be an increase in species frequency of occurrence when there was warming in that period by 0.6 C in the 10 year mean of the average annual temperature at Blue Hill Observatory, as noted above. However, for 23 species that Hosmer (1903) listed as "rather common," "common," or, in one case, "not uncommon," Pratt (1878) either did not list the species in Concord at all, or listed it as "rare," "not common," at only one or two locations, or in some other manner inconsistent with it being "common." Additional support from Thoreau's Journal is provided in Appendix A to support Pratt's (1878) finding rather than Hosmer's (1903) characterization. The explanation for these discrepancies is evident from the discussion earlier in this paper, i.e., that Hosmer (1903) applied a generous concept of "common" to the much wider Concord vicinity rather than to Concord proper. Thus, it is incorrect to use his frequency of occurrence information in all cases and certainly not for the 23 species in this category.

5. Species inappropriate for study. Included in this category are seven species that are either garden escapes, agricultural plants or, in one case, a plant introduced into Concord by Minot Pratt. The story of the rise and decline of *ASPARAGUS OFFICINALIS* included here is given to illustrate how the increase and decrease of species such of these would have nothing to do with climate change. Similarly, none of the other species here belong in a study claiming to relate species decline to climate change.

6. Not declining, or local to Concord if so. The 57 species included in this group are primarily ones for which the frequency of occurrence for the species is either not declining in Middlesex Fells Reservation and Worcester County or is actually increasing in these locations. While this does not directly establish what the species has been doing in Concord, it means that any decline in Concord would be local to the immediate Concord vicinity and not related to the much more widespread effect of climate change. Most likely these species are not declining and Primack et al. (2009) underreported the recent frequency of occurrence in Concord. For some of the species in this group the evidence from Middlesex Fells Reservation and Worcester County is corroborated by recent observations of Concord residents. One species, *LEONURUS CARDIACA* (a once in-favor but now out-of-favor garden plant), in this group could equally well be placed in category 4. None of these species should be used to establish a correlation of "decline" with the absence of significant, historical shifts in flowering time.

7. Possibly declining, but locally if so. The 40 species in this group are ones that are not declining (in some cases they are increasing) in Worcester County but are declining in Middlesex Fells Reservation or were never recorded at the Reservation. In addition, for these species the information from Eaton (1974) generally does not show a significant decrease from the information of Pratt (1878) or Hosmer (1903). Thus any decline in Concord would be local and relatively recent (after 1974). For *Clintonia borealis*, one of my recent observations in Concord is noted and additional information is provided in Appendix A and the Literature Cited to show how significant recent deer-browsing is likely to be the cause for any for this particular species. Also, there is an urbanization gradient that proceeds from Middlesex Fells Reservation through Concord to Worcester County. This gradient has grown through the period under consideration (ca. 1860 to ca. 2004) such that it is to be expected that plant species most affected by urbanization/suburbanization would suffer most in Middlesex Fells

Reservation and least in Worcester County. Species of this type would more likely be found in this group. Whatever the reasons for local declines, such declines would not be due to climate change.

8. Probably declining, but locally if so. The five species in this category are ones for which there is some clear indication in decline outside of Concord, but not in both Worcester County and Middlesex Fells, and for which specific causes other than climate change are not reasonably certain.

9. Declined due to specific causes. The decline of the three species in this category is easily attributable to specific causes as described in Appendix A, not related to climate change.

10. Declining, likely due to causes other than climate warming and/or only locally. The reasons for placement of 16 species in this category are explained in Appendix A. Some of these were disappearing or disappeared well before climate warming would have been significantly operating. Four of the species are not declining in Worcester County.

11. Declining for uncertain reasons. Included here are 20 species that appear to be declining regionally for reasons not known with certainty.

To summarize the results:

51 species not usable or not appropriate for study (categories 1 to 5)
57 species not declining in frequency of occurrence or only locally so (category 6)
40 species possibly declining in frequency of occurrence, but locally if so (category 7)
5 species probably declining in frequency of occurrence, but locally if so (category 8)
19 species declined or declining, but not due to climate change (categories 9 and 10)
20 species declining in frequency of occurrence for unknown reasons (category 11)
192 total (used by Willis et al. (2009) that are claimed as significantly declined)

Thus, instead of 192 species, there are only 20 species to consider whose decline might be significantly related to climate change. The reason (or reasons) for decline of these 20 species in Concord and adjacent regions is an open question. Also, it is not claimed here that climate change has had no role in the decline in Concord of other species, only that climate change would not be the predominant cause. For the purposes of making correlations among the 20 species with responsiveness of flowering time to changes in average temperature, the sample size would appear to be too small. More interesting would be to examine what changes might be occurring at the northern and southern limits of the range of the 20 species, and even in the center (latitudinally) of their range of distribution. Another question is why certain native species, such as *Hibiscus moscheutos*, *Vernonia noveboracensis*, and *Viola brittoniana*, at the northern limit of their range in Concord do not appear to be increasing or decreasing in abundance.

In summary this article shows that the Concord species declines reported by Primack et al. (2009) are unreliable, and in any event they are significantly fewer than the number reported. Because of the unreliability and much smaller number of these claimed declines, the conclusions of Willis et al. (2008) are unjustifiable. This finding in fact helps account for a result differing from that of Willis et al. (2008) found by Bertin (pers. comm. 2014) in a new, forthcoming, detailed analysis of phenology and abundance changes for 186 species over the past 60 years using more than 25,000 herbarium specimens and personal observations. While measurable shifts in flowering times were found for some species over this period, Bertin found no significant correlation, negative or positive, between shift or lack of shift in flowering time and change in abundance. This finding by Bertin is consistent with what is reported here, that the Willis et al. 2008 result is not reliable.

The emerging picture is that only about 44 species among the 429 species selected by Willis et al. (2008) can be determined as probably or definitely declining significantly, but that climate change would not be the predominant cause for 24 of them. Of the remaining 20 for which the cause (or causes) of decline is an open question, 16 species are among the families containing phenologically challenged species. This is more than the 12 species or so that would be estimated by chance (62% noted above), but this is a small sample size. While climate change is likely to be having some effect on the Concord flora, it apparently is not the cause of a dramatic disappearance of species claimed by Primack et al. (2009), even if species of certain groups might be more affected than others as claimed by Willis et al. (2008).

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APPENDIX A

Review of the 192 Concord species used by Willis et al. (2008) claimed by Primack et al. (2009) to have experienced significant decline since 1903 (Hosmer 1903)

Explanation:

Nomenclature is that of my online Concord flora (Angelo 2014b). Where there is a difference, scientific names used in an unpublished spreadsheet used for (Willis et al. 2008), kindly provided by Willis, are given in parentheses.

Names in upper case are not native to Concord.

"MdsxFls: occasional => rare" means at Middlesex Fells Reservation occasional in 1895 and rare in 2012 according to Hamlin et al. (2012) as updated through July 2014 (Hamlin & Kittredge 2013, Hamlin & Kittredge 2014, Hamlin pers. comm. 2014).

"MdsxFls: none => none" means at Middlesex Fells Reservation not found in 1895 and not found in 2012 though elsewhere recorded or reported at the Reservation according to Hamlin et al. (2012).

"MdsxFls no records" means never recorded as found at Middlesex Fells Reservation according to Hamlin et al. (2012).

"WorCo: fairly common not declining (-0.200)" means reported as fairly common in Worcester County in 2012 with no indication of decline, using (Bertin & Rawinski 2012) and the change index (explained previously) for Worcester County, Massachusetts defined in (Bertin 2013) and (Bertin & Parise 2014), where here values between -0.250 and 0.250 are considered not declining.

1. NOT LISTED BY HOSMER (1903) UNDER ANY NAME (4 species)

Lechea tenuifolia: This species is not listed by Hosmer (1903). This name was available to him in Gray's Manual of Botany 6th ed. (Gray et al. 1889) if he had wanted to use it. Hosmer (1903) lists *Lechea minor* and *Lechea thymifolia* both of which would translate into the modern *Lechea intermedia*. *Lechea minor* in the modern sense has not been recorded from Middlesex County. The only other *Lechea* listed by Hosmer (2013) is *Lechea major* which is currently known as *Lechea mucronata*.

MENTHA ARVENSIS: Hosmer (1903) does not list this under any name.

MONARDA BRADBURIANA: Hosmer (1903) does not list this. If *MONARDA FISTULOSA* is intended by Primack et al. (2009), then this is a Minot Pratt introduction and not suitable for study.

MONARDA MEDIA: Hosmer (1903) and Pratt (1878) do not list this from Concord. Thoreau does not refer to it in his Journal and collected no herbarium specimen of it.

2. TAXONOMIC PROBLEMS (8 species)

Agrimonia gryposepala: Hosmer's (1903) use of this name includes *Agrimonia gryposepala* and *Agrimonia stricta*. Thus, his frequency information is not usable.

Antennaria plantaginifolia: Hosmer's (1903) use of this name includes *Antennaria plantaginifolia*, *Antennaria howellii* subsp. *neodioica*, *Antennaria neglecta*, *Antennaria parlinii* var. *parlinii*, and almost certainly *Antennaria parlinii* var. *fallax*. Thus, his frequency information is not usable.

Galium trifidum: Hosmer's (1903) use of this name includes *Galium trifidum*, *Galium palustre*, and *Galium tinctorum*. Thus, his frequency information is not usable.

Gentiana andrewsii: Hosmer's (1903) use of this name includes *Gentiana andrewsii* and *Gentiana clausa*. Thus, his frequency information is not usable.

MENTHA PIPERITA: This is a hybrid (*MENTHA AQUATICA* X *MENTHA SPICATA*) and not a proper taxon for a study of this type.

Rosa carolina: Hosmer's (1903) use of this name includes *Rosa carolina* and *Rosa virginiana*. Thus, his frequency information is not usable.

Rosa virginiana: This name is not used by Hosmer (1903) as he would have included it in *Rosa carolina* as noted above. Which of Hosmer's (1903) names Willis et al. (2008) or Primack et al. (2009) translated into this name is unclear. *Rosa virginiana* is not declining (or only in Concord if so) in any event. MdsxFls: frequent => frequent. WorCo: fairly common not declining (-0.160).

Viola blanda: Hosmer's (1903) use of this name includes *Viola blanda* and *Viola macloskeyi*. Thus, his frequency information is not usable.

3. NO FREQUENCY INFORMATION PROVIDED BY HOSMER (1903) (9 species)

Asclepias exaltata: Hosmer (1903) lists this as "Swamps." Pratt (1878) lists this as rare with only three to four plants in total located in a certain sector of Concord. Thoreau refers to this only twice in his Journal only one of which is to occurrence in Concord. Hence, there is very minimal occurrence in Concord to begin with. MdsxFls: rare => occasional. WorCo: common not declining (0.026).

Geum aleppicum: Hosmer (1903) lists this (as *Geum strictum*) without comment. MdsxFls: no records. WorCo: uncommon not declining (-0.200). Cole Winstanley (2014 pers. comm.) recently photographed this near Elm Brook. Cherrie Corey (2014 pers. comm.) reports this recently at Great Meadows occurring each year reliably in good quantity all along the Dike Trail and also found near the Ripley building.

LILIUM LANCIFOLIUM: Hosmer (1903) lists this simply as "Escaped." Also, this occasional garden escape is not appropriate for study. MdsxFls: no records. WorCo: uncommon decreasing (-0.27)

Persicaria punctata (Polygonum punctatum): Hosmer (1903) lists this only as "River." MdsxFls: rare => rare. WorCo: common increasing (0.681).

Platanthera clavellata: Hosmer (1903) lists this (as *Habenaria tridentata*) with no frequency information. MdsxFls: no records. WorCo: fairly common not declining (-0.120).

Rumex brittanica (*Rumex orbiculatus*): Hosmer (1903) lists this only as "Brooks." MdsxFls: no records. WorCo: fairly common increasing (0.429).

Sagittaria filiformis (*Sagittaria subulata*): Hosmer (1903) lists this only as "River." MdsxFls: no records. WorCo: rare increasing (0.333), all records from the county are after 1973.

Utricularia purpurea: Hosmer (1903) lists this only as "River." MdsxFls: rare => none. WorCo: common increasing (0.353).

Vaccinium oxycoccus: Hosmer (1903) lists this only as "Cold swamps." MdsxFls: no records. WorCo: fairly common not declining (0.100).

4. HOSMER (1903) FREQUENCY INFORMATION CONFLICTS WITH PRATT (1878) AND WITH THOREAU (23 species)

ANAGALLIS ARVENSIS: Hosmer (1903) lists this as common. Not listed at all by Pratt (1878). No specimen in Thoreau herbarium, and only two references in Thoreau Journal neither of which are to occurrence in Concord. Middlesex County Flora (Dame & Collins 1888) has this as rare, found in only two towns, not Concord. MdsxFls: no records. WorCo: rare, first record in 1933.

Angelica atropurpurea: Hosmer (1903) lists this as common. Pratt (1878) lists only two locations for it, Thoreau's Journal refers to it mostly or entirely at two locales in the town. Middlesex County Flora (Dame & Collins 1888) has this as generally distributed, but scarce. MdsxFls: no records. WorCo: fairly common not declining (-0.143).

Apocynum cannabinum: Hosmer (1903) lists it as common. Pratt (1878) lists this as rare, Middlesex County Flora (Dame & Collins 1888) has this as not common. MdsxFls: rare => rare. WorCo: common increasing (0.560).

ARMORACIA RUSTICANA: Hosmer (1903) lists this as rather common. Pratt (1878) does not list this at all. Thoreau refers to it only four times in his Journal with no definite reference to wild occurrence and no specimen of it in his herbarium. MdsxFls: no records. WorCo: rare declining (-0.64).

Asclepias purpurascens: Hosmer (1903) lists this as common. Pratt (1878) lists it as rare. No specimen in Thoreau herbarium and only one Journal reference to it in Concord, which itself is likely a mistaken identification. MdsxFls: no records. WorCo: presumed extirpated formerly sporadic, last record 1954.

Chenopodium simplex: Hosmer (1903) lists this as common. Pratt (1878) however lists it as not common. Thoreau mentions it only four times in his Journal. MdsxFls: rare => occasional. WorCo: uncommon increasing (0.286).

Circaea alpina: Hosmer (1903) lists this as common. Pratt (1878) lists it from only two locations in Concord. Thoreau refers to it only about nine times in his Journal, but the inadequacy of the manuals he used make is identifications questionable, especially since he refers to the more common *Circaea canadensis* only seven times. MdsxFls: no records. WorCo: fairly common not declining (0.235).

Crotalaria sagittalis: Hosmer (1903) lists this as rather common. Pratt (1878) lists it as rare. Thoreau notes it at a few sites in Concord and late in his life (October 3, 1858) comments in his Journal "One year I find it on the Great Fields and think it rare; the next I find it in a new and unexpected place. It flits about like a flock of sparrows, from field to field." MdsxFls: no records. WorCo: rare increasing, first record in the 2000s.

FAGOPYRUM ESCULENTUM: Hosmer (1903) is the only one to list this escape from cultivation as common. Thoreau refers to it only twice in his Journal. Pratt (1878) lists it without commenting on its frequency. Eaton (1974) refers to it only as occasional, rarely persistent after cultivation. Also, any decrease in frequency would be most likely associated with decrease in its cultivation. MdsxFls: rare => none. WorCo: uncommon not declining (-0.23).

Goodyera tesselata: Hosmer (1903) lists this as rather common. Pratt (1878) lists it as rare. There are only six references to it in Thoreau's Journal with only two locales mentioned and no specimen in his herbarium. MdsxFls: no records. WorCo: fairly common not declining (-0.222).

HYLOTELEPHIUM TELEPHIUM (*HYLOTELEPHIUM TELEPHIOIDES*, in error): Hosmer (1903) lists this as common. Pratt (1878) notes it at only one location. There are nine references (one in error) to this in Thoreau's Journal with only one location specified in multiple references. MdsxFls: occasional => occasional. WorCo: common increasing (0.30).

Iris prismatica: Hosmer (1903) lists this as common. Pratt (1878) lists it as not as common as *Iris versicolor* which he lists as common. There are only eight references to this in Thoreau's Journal in which no more than two Concord locations are specified. MdsxFls: no records. WorCo: presumed extirpated, only record from 1937.

Myosotis verna: Hosmer (1903) lists this as common. Pratt (1878) lists it from just two locales. Thoreau refers to it only seven times in his Journal, all apparently at Conantum where he found it in several places. Eaton (1974) lists this as uncommon. MdsxFls: frequent => rare. WorCo: rare declining (-0.333).

Prenanthes serpentaria: Hosmer (1903) lists this as common. Pratt (1878) lists only one location for it. Only five references to it in Thoreau's Journal and only two Concord locations noted. MdsxFls: rare => rare. WorCo: presumably extirpated, last record 1935.

Pycnanthemum incanum: Hosmer (1903) lists this as rather common. Pratt (1878) lists only two locations. Thoreau only refers to it seven times in his Journal with only two Concord locations noted. MdsxFls: none => rare. WorCo: uncommon increasing, all records after 1987.

Pycnanthemum muticum: Hosmer (1903) lists this as common. Pratt (1878) does not list it at all. Thoreau refers to it only seven times in his Journal noting apparently three Concord locations. MdsxFls: no records. WorCo: uncommon decreasing (-0.300).

Pyrola chlorantha: Hosmer (1903) lists this as common. Pratt (1878) lists just two locations. Thoreau refers to it only six times in his journal noting just two Concord locations. MdsxFls: rare => none. WorCo: uncommon declining (-.333).

RIBES RUBRUM: Hosmer (1903) lists this as common. Pratt (1878) does not list it at all. Thoreau's Journal has no references to it in the wild and no specimen is in his herbarium. Also, any decline would likely be due to purposeful eradication of *Ribes* spp. to prevent pine blister rust in the 20th century. MdsxFls: rare => rare. WorCo: common not declining (0.06).

Sericocarpus limifolius: Hosmer (1903) lists this as common. Pratt (1878) does not list it at all. No references to it in Thoreau's Journal. MdsxFls: rare => rare. WorCo: uncommon not declining (0.091).

SILENE ARMERIA: Hosmer (1903) lists this as rather common. Pratt (1878) lists it as only occasionally wild. Thoreau refers to it only three times in his Journal and no specimen in his herbarium. MdsxFls: none => occasional. WorCo: fairly common not declining (0.15).

Solidago uliginosa: Hosmer (1903) lists this as common. Pratt (1878) lists it simply as in swamps in the north part of town with no indication that it is common. There is only one reference to this in Thoreau's Journal. MdsxFls: rare => rare. WorCo: common not declining (0.091).

Tephrosia virginiana: Hosmer (1903) lists this as not uncommon. Pratt (1878) lists this as rather rare. Thoreau's Journal does not refer to more than perhaps three Concord locations for it. MdsxFls: no records. WorCo: uncommon not declining (0.111).

Vernonia noveboracensis: Hosmer (1903) lists this as common. Pratt (1878) lists this as rather rare. Thoreau's Journal refers to this only at Flint's Bridge and along the Assabet River "here and there." MdsxFls: no records. WorCo: rare declining (-0.429).

5. SPECIES INAPPROPRIATE FOR STUDY (7 species)

ASPARAGUS OFFICINALIS: Eaton (1974) notes this to be common as single plants apparently spread by birds. Thoreau refers to it only four times in his Journal and collected no specimen in his herbarium. Its history in Concord is easily explained by the advent and subsequent decline of

asparagus farming in Concord after Thoreau (see quote below). MdsxFls: no records. WorCo: common not declining (0.07).

"It was about this time that the production of asparagus exploded. Between 1876 and 1879 ground planted to asparagus doubled. In the early asparagus years in the late 1870s the largest producers were mostly on Sudbury Road led by George Wheeler, Judge French and Charles Hubbard. Bob Gross called Concord 'the asparagus capital of the Guilded [sic] Age'. By the 1880s Concord produced 75,000 bunches of asparagus, half the Massachusetts crop. The Middlesex County Asparagus Growers Association later registered the Old North Bridge brand of asparagus." --<http://www.concordma.com/magazine/autumn07/19centuryfarming.html>

Even in my time in the 1970s/80s there was Asparagus Farm on Bedford Street. But this farm is gone and asparagus farming, while still conducted in Concord, is very much reduced.

CAMPANULA ROTUNDIFOLIA: This was introduced to Concord by Minot Pratt. No Journal reference to this or herbarium collection by Thoreau in Concord.

MALVA NEGLECTA: Only four references to this in Thoreau's Journal. However, Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. This is a weed of lawns, barnyards and cultivated fields. MdsxFls: occasional => rare. WorCo: fairly common not declining (-0.03).

PASTINACA SATIVA: This is an agricultural plant. The historical information is inconsistent. Hosmer (1903) lists this as common. Pratt (1878) lists one locale "and other places." Thoreau refers to it about eight times in his Journal with one locale in an orchard and almost none of the others with specific locale. MdsxFls: occasional => none. WorCo: fairly common not declining (0.08).

PERSICARIA ORIENTALIS (*POLYGONUM ORIENTALE*): Pratt (1878) lists this as often cultivated, but occasionally found spontaneous. Hosmer (1903) lists this from dumps and apparently one Concord location (but possibly in Lincoln). This is an occasional garden escape. MdsxFls: no records. WorCo: presumed extirpated and never established, last record 1945.

PORTULACA OLERACEA: Thoreau refers to it only eleven times in his Journal. Pratt (1878) lists it without commenting on frequency. Hosmer (1903) lists it as very common. Eaton (1974) lists it as common, often abundant. This is a garden, yard and cultivated land weed that increased significantly since Thoreau's time. MdsxFls: common => frequent. WorCo: common increasing (0.62).

SPERGULA ARVENSIS: There are just seven references to this in Thoreau's Journal with no more than 3-4 locales of wild occurrence in Concord implied. Pratt (1878) lists it without providing frequency information. Hosmer (1903) lists this as common. Eaton (1974) lists it as uncommon. This weed is associated with cultivated fields. MdsxFls: no records. WorCo: uncommon declining (-0.57).

6. NOT DECLINING, OR LOCAL TO CONCORD IF SO (57 species)

Allium canadense: MdsxFls: rare => frequent. WorCo: uncommon not declining (-0.048). Hosmer (1903) lists this as common. Pratt (1878) lists this from only two sites. Thoreau refers to it only about ten times in his Journal mentioning only three Concord locations specifically.

Anemone quinquefolia: MdsxFls: common => common. WorCo: common not declining (0.105). Cherrie Corey (2014 pers. comm.) reports this to be currently one of the most abundant spring flowers in Concord with many more than four stations.

Apios americana: MdsxFls: frequent => common. WorCo: common not declining (0.091). Cherrie Corey (2014 pers. comm.) reports this to be currently plentiful in Concord with many more than four stations.

Aralia hispida: MdsxFls: common => common. WorCo: common not declining (0.237).

Aureolaria flava: MdsxFl: none => occasional. WorCo: fairly common not declining (-.0161).

Aureolaria pedicularia: MdsxFls: frequent => common. WorCo: common not declining (0.241).

BERBERIS VULGARIS: MdsxFls: common => common. WorCo: common not declining (0.11).

Chimaphila umbellata: MdsxFls: frequent => common. WorCo: common not declining (-0.034). Cherrie Corey (2014 pers. comm.) reports more than four stations of this currently in Concord. Cole Winstanley (2014 pers. comm.) reports more than six stations in the Estabrook Woods alone.

Chrysosplenium americanum: MdsxFls: frequent => frequent. WorCo: common increasing (0.333).

Comandra umbellata: MdsxFls: common => common. WorCo: common not declining (0.026).

Comptonia peregrina: MdsxFls: common => common. WorCo: common not declining (0.026).

Cornus alternifolia: MdsxFls: common => common. WorCo: common not declining (0.242). Cherrie Corey (2014 pers. comm.) reports this to be currently common in Concord.

Cornus rugosa: MdsxFls: rare => rare. WorCo: fairly common not declining (0.243). Eaton (1974) reported this as infrequent. Yet I found it in five locations in the 1970s/80s. In 2014 Cherrie Corey (2014 pers. comm.) found this in two locations different from my locations.

Epilobium coloratum: MdsxFls: none => rare. WorCo: common not declining (0.088).

Eubotrys racemosa: MdsxFls: frequent => frequent. WorCo: fairly not declining (0.231). Hosmer (1903) lists this as uncommon. Pratt (1878) does not list this from Concord. Thoreau refers to it about nine times in his Journal, but all references to it in Concord are from one site. The site where Thoreau saw it, a *Chamaecyparis* swamp, was significantly ruined about 1940 according to Eaton (1974). Hosmer's (1903) information is inadequate to determine how many stations he knew it from in Concord. I found this in the 1980s at a site not known to Thoreau or Minot Pratt.

Eupatorium perfoliatum: MdsxFls: common => common. WorCo: common not declining (0.113).

Euphorbia maculata (*Chamaesyce nutans*): MdsxFls: rare => frequent. WorCo: common increasing (0.341). Cherrie Corey (2014 pers. comm.) reports this to be currently very common in Concord.

Eurybia macrophylla: MdsxFls: occasional => common. WorCo: common not declining (0.024). Cherrie Corey (2014 pers. comm.) reports this to be currently common in Concord.

Gaultheria procumbens: MdsxFls: common => common. WorCo: common not declining (0.044). Cherrie Corey (2014 pers. comm.) reports this currently plentiful with many more than four stations, robust at Moore's Swamp, for example.

Goodyera pubescens: Cherrie Corey (2014 pers. comm.) has seen and photographed this in more than four locales in Concord in recent years. Cole Winstanley (2014 pers. comm.) has observed more than four stations in Estabrook Woods alone. MdsxFls: occasional => none. WorCo: common not declining (0.143).

Gratiola aurea: MdsxFls: frequent => frequent. WorCo: common not declining (0.176).

Hieracium scabrum: MdsxFls: frequent => common. WorCo: common not declining (0.183).

Houstonia caerulea (moist fields, pastures): Hosmer (1903) lists this as very common. Eaton (1974) lists it as common. I found this common in the 1980s. In recent years Cherrie Corey (2014 pers. comm.) has found large numbers of these in many places in Sleepy Hollow Cemetery, a patch every year at Great Meadows, abundant at a cul-de-sac near Route 2, patches at the former landfill by Route 2, small patches near Walden Pond, patches along a Park Service Trail near Meriam's Corner, and other places not noted -- finding one or two new locations each year. Cole Winstanley (pers. comm. 2014) notes two additional locations and is aware of others not noted by him since it is so common. Any decline in this is in Concord is minimal. MdsxFls: common => rare. WorCo: common not declining (0.053).

Hypoxis hirsuta: MdsxFls: common => common. WorCo: common not declining (-0.054). Cherrie Corey (2014 pers. comm.) reports it to be currently plentiful at the lime quarries in the Estabrook Woods. Cole Winstanley (2014 pers. comm.) reports this recently along a trail in the northern part of Estabrook Woods.

Ilex verticillata: MdsxFls: common => common. WorCo: common not declining (0.132). Cherrie Corey (2014 pers. comm.) reports this to be currently very common in Concord. Cole Winstanley (2014 pers. comm.) reports from many wooded swamps, at least in the Estabrook and Wright woods. Bryan Hamlin (pers. comm. 2014) reports this as one of the common species missed by Drayton & Primack (1996) in their Middlesex Fells study.

Kalmia latifolia: MdsxFls: none => frequent. WorCo: abundant not declining (0.028).

LEONURUS CARDIACA: MdsxFls: occasional => frequent. WorCo: common not declining (0.23). Hosmer (1903) lists this as common, but there are only three references to it in Thoreau's Journal and Pratt (1878) does not comment on frequency.

Lespedeza hirta: MdsxFls: frequent => common. WorCo: common not declining (0.195).

Lilium canadense: MdsxFls: frequent => frequent. WorCo: common not declining (0.039).

Ludwigia palustris: MdsxFls: common => common. WorCo: common not declining (0.124).

Mitchella repens: MdsxFls: common => common. WorCo: common not declining (0.176). Cherrie Corey (2014 pers. comm.) and Cole Winstanley (2014 pers. comm.) both report this currently plentiful, easily with many more than five locations, generally in mixed pine-oak forest throughout Concord.

Monotropa hypopitys: MdsxFls: frequent => frequent. WorCo: uncommon increasing (0.371). Hosmer (1903) lists this as common. Pratt (1878) lists this as rare. Thoreau notes it in his Journal at six locations in Concord. Cherrie Corey (2014 pers. comm.) reports seeing this recently in the Spencer Brook Valley and since 2008 southwest of Gowing's Swamp and in the Estabrook Woods.

Myrica gale: MdsxFls: occasional => none. WorCo: common not declining (0.140). The frequency information used by Willis et al. (2008) from Primack et al. (2009) was its complete absence from Concord. In 2007 I verified it (and directed the lead author of the latter study to it) plentiful at a roadside location that I knew from the 1970s, and that was the only location for it cited by Pratt (1878). Cherrie Corey (2014 pers. comm.) reports two different healthy populations of it there and 4-5 distinct populations at Great Meadows. Eaton (1974) lists it as common.

Nymphoides cordata: MdsxFls: no records. WorCo: fairly common not declining (0.063).

Penthorum sedoides: MdsxFls: occasional => occasional. WorCo: common increasing (0.265). Eaton (1974) indicates that this is scarce, formerly common, and possibly a casualty of river pollution. Decline in Concord and not elsewhere is consistent with river pollution particular to Concord.

Persicaria sagittata (*Polygonum sagittatum*): MdsxFls: common => common. WorCo: common not declining (0.062). Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. Cherrie Corey (2014 pers. comm.) reports this to be currently pervasive at Great Meadows also generally in the floodplain of the Concord River.

Polygonatum pubescens: MdsxFls: common => common. WorCo: common not declining (0.132).

Proserpinaca palustris: MdsxFls: occasional => frequent. WorCo: common, not declining (0.088).

Prunella vulgaris: MdsxFls: common => common. WorCo: common not declining.

Prunus virginiana: MdsxFls: common => common. WorCo: common not declining (0.054).

Sassafras albidum: MdsxFls: frequent => common. WorCo: common not declining (0.118). Currently widespread in Concord according to Cherrie Corey (2014 pers. comm.) and Cole Winstanley (2014 pers. comm.) who between them know of at least 12 stations for it.

Scorzoneroides autumnalis (Leontodon autumnalis): MdsxFls: common => common. WorCo: common not declining (0.24).

Silene antirrhina: MdsxFls: occasional => occasional. WorCo: common increasing (0.409).

Sium suave: MdsxFls: common => common. WorCo: common not declining (0.194). Cherrie Corey (2014 pers. comm.) reports this currently plentiful in Concord with many more than four stations.

Smilax herbacea: MdsxFls: frequent => common. WorCo: common not declining (0.107). Cherrie Corey (2014 pers. comm.) reports this to be currently common in Concord. Cole Winstanley (2014 pers. comm.) reports more than seven stations, more than six in Estabrook Woods alone.

Solidago bicolor: MdsxFls: common => common. WorCo: common not declining (-0.018).

Sparganium eurycarpum: MdsxFls: no records. WorCo: uncommon increasing (0.500). Hosmer (1903) lists this as common. Pratt (1878) lists it without commenting on frequency. There are only four references to this in Thoreau's Journal. Eaton (1974) lists it as common along the banks of the polluted river. The most likely explanation is that it was uncommon in Thoreau's time, later became more common in the Concord vicinity due to manufacturing pollution in the rivers in the late 19th century and later sewage pollution in Concord in the 1930s, and is likely uncommon again due to

improvement of the river water quality in recent decades. Cherrie Corey (2014 pers. comm.) reports this to be increasing at Great Meadows over the past eight years.

Symphyotrichum novae-angliae: MdsxFls: none => rare. WorCo: common not declining (0.135). Thoreau never saw this in Concord. There are three references to it in his Journal, none of which refer to Concord. Late in his life (September 16, 1859) he notes in his Journal finding it in neighboring Acton and commenting "I must call it a plant of this vicinity, then." Pratt (1878) lists it as abundant at one locality in Concord and rare in other parts of the town. Hosmer (1903) simply lists this at three localities in Concord. Eaton lists it as common, rapidly increasing in abundance. Cherrie Corey (2014 pers. comm.) reports this currently to be in at least four locations in Concord.

Symphyotrichum puniceum: MdsxFls: frequent => frequent. WorCo: common not declining (0.196).

Symphyotrichum undulatum: MdsxFls: common => common. WorCo: common not declining (0.013).

Triadenum virginicum: MdsxFls: frequent => common. WorCo: common increasing (0.582). Cherrie Corey (2014 pers. comm.) reports this as currently common in Concord.

TRIFOLIUM CAMPESTRE: MdsxFls: none => frequent. WorCo: fairly common increasing (0.71).

Utricularia gibba: MdsxFls: rare => rare. WorCo: common increasing (0.408). Hosmer (1903) lists this at only one possible Concord locality, Fairhaven Bay, but that bay has a Lincoln side as well as a Concord side divided about equally. Hosmer's reference to this at Grassy Pond is a well-known locality in Acton, Massachusetts. Pratt (1878) does not list this species for Concord. There are no references to it in Thoreau's Journal and no specimen in his herbarium. Edward Hoar collected a specimen in Bateman's Pond only in 1875. Eaton lists it as common, abundant in the Great Meadows impoundments created well after Thoreau's time. The record shows that this was essentially absent from Concord in Thoreau's and Pratt's time and increased significantly in abundance after Hosmer's time.

Utricularia radiata (*Utricularia inflata*): MdsxFls: none => occasional. WorCo: common not declining (0.129).

Veratrum viride: MdsxFls: frequent => occasional. WorCo: common increasing (0.429).
Currently common in Concord. Cherrie Corey (2014 pers. comm.) has found this growing abundantly in many wet seeps in the Estabrook Woods, especially in the upper Saw Mill Brook area and the drainage from Mink Pond and frequent throughout the upper Spencer Brook valley (in 2014). I found this in a different location in the southwest part of Concord on a brief visit in 2007.

Verbena urticifolia: MdsxFls: frequent => common. WorCo: common not declining (0.122). Cherrie Corey (2014 pers. comm.) reports this to be currently common in Concord.

Viburnum lentago: MdsxFls: frequent => frequent. WorCo: common not declining (0.118).

7. POSSIBLY DECLINING, BUT LOCALLY IF SO (40 species)

Baptisia tinctoria: Pratt (1878) and Eaton (1974) list this as common. Hosmer (1903) lists it as very common. MdsxFls: common => frequent. WorCo: common not declining (0.022).

Bidens cernua: Hosmer (1903) and Eaton (1974) list this as common. Cherrie Corey (2014 pers. common.) reports this to be currently common in Concord. MdsxFls: frequent => rare. WorCo: common not declining (0.013).

Campanula aparinoides: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as frequent. MdsxFls: occasional => none. WorCo: fairly common not declining (-0.182).

Cardamine pensylvanica: Hosmer (1903) and Eaton (1974) list this as common. Cherrie Corey (2014 pers. comm.) reports this becoming a noxious weed at roadsides, fields and lawns throughout Concord. MdsxFls: common => frequent. WorCo: common not declining (0.200).

CIRSIUM VULGARE: Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => frequent. WorCo: fairly common increasing (0.44), first collected in 1901.

Clematis virginiana: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as uncommon. Cherrie Corey (2014 pers. comm.) and Cole Winstanley (2014 pers. comm.) have three stations for this currently in Concord. Primack et al. (2009) found this at a different location than the other three, so that under the definition of "common" adopted for that study and by Willis et al. (2008) this qualifies currently as "common." MdsxFls: frequent => rare. WorCo: common not declining (0.084).

Clintonia borealis: Pratt (1878) simply notes it in Walden Woods and elsewhere. Eaton (1974) lists it as frequent. One Concord population was found unexpectedly by me during a brief visit in 2007. Deer browsing is most likely the reason for any decline in this species. Waller & Alverson (1997) found this species to be particularly vulnerable among other Liliaceae to deer browsing in Wisconsin, in one instance having extirpated it from a large island there. Also, Balgooyen & Waller (1995) have shown that this species in particular can be used as a good indicator of deer browsing activity. MdsxFls: no records. WorCo: common not declining (-0.012).

Cornus racemosa: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. Cherrie Corey (2014 pers. comm.) reports this to be currently in at least four locations in Concord. MdsxFls: common => frequent. WorCo: common not declining (0.200).

Drosera intermedia: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: frequent => none. WorCo: common increasing (0.373).

Gnaphalium uliginosum: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => frequent. WorCo: common not declining (0.07).

Hedeoma pulegioides (dry rocky woods, fields and old pastures): Eaton (1974) lists this as infrequent, but abundant in the Conantum vicinity. MdsxFls: common => occasional. WorCo: fairly common not declining (-0.189).

Hieracium venosum: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => frequent. WorCo: fairly common not declining (0.095).

Hylodesmum nudiflorum (*Desmodium nudiflorum*): Hosmer (1903) lists this as common. Pratt (1878) lists it for two locales and sparsely in other places. Thoreau refers to this only five times in his Journal and notes it at only one Concord locale. Eaton (1974) listed this as rare. In the 1970s/80s I found this in five locations including one of those listed by Pratt (1878) and the one noted by Thoreau.

The great variation in ability of botanists to find this is notable. MdsxFls: frequent => occasional. WorCo: fairly common not declining (0.158).

Hypericum canadense: Pratt (1878) lists this as rather common. Hosmer (1903) lists it as very common. Eaton (1974) lists this as frequent. MdsxFls: common => frequent. WorCo: common not declining (0.158).

Hypericum gentianoides: Hosmer (1903) lists this as very common. Eaton (1974) lists it as common. MdsxFls: common => frequent. WorCo: common not declining (0.234).

Kalmia polifolia: Thoreau in his Journal indicates that he found this in four Concord bogs, two of which were later ruined in the first half of the 20th century. Pratt (1878) lists this as rare found in only a few cold bogs. Hosmer (1903) simply lists this from three bogs -- two in Concord and the other mostly in Lincoln. Eaton (1974) lists this as occasional, at four stations (three of Thoreau's and one not cited by the others). In the 1970s/80s I found this in five Concord bogs. If two bogs where Thoreau saw it had not been ruined before my time, I would have seen it in seven bogs. On the surface the evidence suggests that this species increased in frequency between historic times and even between my time and Eaton. Observer reports are variable. It is known to survive in at least one of the bogs in recent years, but unless the other four bogs where I saw it are searched by a competent botanist and the bogs observed for degradation, this species cannot be determined to have declined. Any decline is most likely due to degradation of bogs and would be local in any case. MdsxFls: no records. WorCo: uncommon not declining (0.040).

Lechea intermedia: Hosmer (1903) lists this under two separate names as common. Eaton (1974) lists it as common. MdsxFls: frequent => occasional. WorCo: common not declining (0.157).

Lechea mucronata: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => rare. WorCo: common increasing (0.375). Cherrie Corey (2014 pers. comm.) reports this to be currently common in Concord.

Lobelia inflata: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. Cherrie Corey (2014 pers. comm.) reports this to be currently at many stations in Concord, sporadic in waste areas. MdsxFls: common => frequent. WorCo: common not declining (0.073).

Lobelia spicata: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: frequent => none. WorCo: fairly common not declining (0.069).

Lycopus americanus: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists this as frequent. MdsxFls: common => frequent. WorCo: common not declining (0.146).

Micranthes pensylvanica (*Saxifraga pensylvanica*): Pratt (1878) lists this as common. Hosmer (1903) lists it as very common. Eaton (1974) lists it as frequent. MdsxFls: frequent => none. WorCo: common, not declining (0.033).

NEPETA CATARIA: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as uncommon. MdsxFls: occasional => rare. WorCo: fairly common not declining (-0.14).

Packera aurea: Pratt (1878) lists this as common. Hosmer (1903) lists it as very common. Eaton (1974) lists it as frequent. MdsxFls: common => occasional. WorCo: common not declining (0.157).

Platanthera grandiflora: Thoreau refers to this 11 times in his journal, but all Concord occurrences are at one location. Pratt (1878) lists this as rare, but adds that it is occasionally found in boggy places. Hosmer (1903) lists this as rather uncommon and notes only one Concord locality. Whether Hosmer knew any other localities in Concord is unknown. Eaton (1974) lists it as occasional. I confirmed this in Concord in 2007 in about the same quantity (seven plants or more) where I had seen it in the 1970s, but was unable to check on the two other locations where I had seen it more sparsely, one of these being Thoreau's location. MdsxFls: no records. WorCo: fairly common declining (-.300).

Polygala paucifolia: Pratt (1878) lists this as abundant in the south part of town. Hosmer (1903) lists it as common. Eaton (1974) lists it as frequent, often abundant in large colonies. MdsxFls: no records. WorCo: common not declining (0.034).

Polygala sanguinea: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: frequent => occasional. WorCo: common not declining (-0.011).

Sagittaria latifolia: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: frequent => occasional. WorCo: common increasing (0.277).

Sarracenia purpurea: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as rather common. Any decline most likely due to habitat destruction/degradation which would occur more frequently in the more developed urban and suburban metropolitan Boston area. MdsxFls: frequent => none. WorCo: fairly common not declining (-0.040).

Sericocarpus asteroides: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as frequent. MdsxFls: common => frequent. WorCo: common not declining (-0.050).

SISYMBRIUM OFFICINALE: Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => occasional. WorCo: common not declining (0.11).

Spiraea tomentosa: Pratt (1878) lists this as abundant. Hosmer (1903) and Eaton (1974) list it as very common. Cherrie Corey (2014 pers. comm.) reports this to be currently common in Concord. MdsxFls: common => frequent. WorCo: common not declining (0.034).

Spiranthes cernua: Pratt (1878), Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => occasional. WorCo: common not declining (-0.026).

Symphyotrichum patens: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as frequent. MdsxFls: common => rare. WorCo: fairly common increasing (0.391).

Trillium cernuum: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as uncommon. MdsxFls: frequent => occasional. WorCo: common not declining (-0.026).

Trillium undulatum: Hosmer (1903) lists this only from Minot Pratt's property and Stow swamp (in Stow, Massachusetts). The station at Pratt's would be an introduction since Pratt (1878) lists this as rare, found at only one location elsewhere in the Concord. Thoreau himself never saw this in Concord, although his sister did and collected a specimen. Disappearance from Concord of what was likely just one small station is possible, but would most likely be due to habitat destruction or picking and is local in any case. MdsxFls: no records. WorCo: common not declining (-0.059).

Urtica dioica subsp. *gracilis*: Pratt (1878) lists this as not uncommon. Hosmer (1903) and Eaton (1974) list this as common. Thoreau refers to this only five times in his Journal. MdsxFls: common => rare. WorCo: common not declining.

Utricularia cornuta: Hosmer (1903) lists this as "Bateman's Pond. Banks of river." Pratt (1878) notes this simply on the shores of Bateman's Pond. Thoreau refers to this only eight times in his Journal and only notes it at Fairhaven Bay (Sudbury River) about half of which is in Lincoln. The only definite Concord location is Bateman's Pond (as confirmed by Eaton) so that Primack et al. (2009) assigning Hosmer's (1903) frequency of occurrence as "frequent" is unjustified. If this is currently absent from Bateman's Pond, the significance would be minimal and likely due to water quality issues at Bateman's Pond which is now private school property. MdsxFls: no records. WorCo: fairly common increasing (0.333).

Veronica scutellata: Hosmer (1903) and Eaton (1974) list this as common. MdsxFls: common => occasional. WorCo: common not declining (0.014).

Viola labradorica: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as uncommon. Middlesex County Flora (1888) lists this as widely distributed but not common. Thoreau refers to it 11 times in his Journal suggesting he found it infrequent or uncommon. MdsxFls: rare => none. WorCo: common not declining (-0.071).

8. PROBABLY DECLINING, BUT LOCALLY IF SO (5 species)

CIRSIUM ARVENSE (fields, pastures, waste ground): Pratt (1878) lists this as frequent. Hosmer (1903) lists it as very common. Eaton (1974) reports it to be very scarce. MdsxFls: frequent => rare. WorCo: fairly common, not declining (0.11).

Helianthus divaricatus (roadsides, dry thickets and open woods): Pratt (1878) lists this as not uncommon. Hosmer (1903) lists it as common. Eaton (1974) lists this as uncommon. MdsxFls: rare => occasional. WorCo: fairly common declining (-0.373).

Lilium philadelphicum (dry, open, usually deciduous woods and clearings): Pratt (1878) lists this as frequent. Hosmer (1903) lists it as rather common. Eaton (1974) lists this as infrequent but scarce. This is a species probably declining due to disappearance of habitat and to deer browsing, but it is not yet declining in Worcester County. MdsxFls: frequent => none. WorCo: common not declining (-0.104).

Oenothera perennis (fields, clearings): Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as frequent. MdsxFls: common => none. WorCo: common not declining (-0.031).

Symphyotrichum laeve (dry open ground): Pratt (1878) and Hosmer (1903) list this as common. Eaton lists it as uncommon. MdsxFls: common => none. WorCo: common not declining (-0.133).

9. SPECIES DECLINE DUE TO SPECIFIC CAUSES (3 species)

Andromeda polifolia: Decline in Concord attributable to habitat destruction. Hosmer (1903) lists this only from two specific sphagnum bogs in Concord. One of these bogs was ruined in the first part of the 20th century. Dr. Harold Hemond of MIT (2014 pers. comm.) has seen it at the remaining bog in the past few years in quantities many more than 10 plants. Cherrie Corey (2014 pers. comm.) has seen a hundred or more plants at this bog in recent years. MdsxFls: no records. WorCo: rare declining (-0.333).

Celastrus scandens: The dramatic disappearance of this species in eastern Massachusetts and elsewhere can be directly associated with its replacement by the similar alien *CELASTRUS ORBICULATUS* beginning at least by about 1950. Fernald (1950) does not include New England in the range of *CELASTRUS ORBICULATUS*, but Bertin & Rawinski (2012) report the first herbarium collection of it in Worcester County in 1942 and notes that hybridization between the two species is likely contributing to the decline of the native species. I saw a few massive individuals of *CELASTRUS ORBICULATUS* in Concord's Estabrook Woods in the late 1970s that must have been there at least since 1950. Eaton (1974) in error reported *Celastrus scandens* to be "Frequent" without any listing of *CELASTRUS ORBICULATUS* when in fact I found in the late 1970s that *CELASTRUS ORBICULATUS* was ubiquitous and that *Celastrus scandens* was nowhere to be found. So, the replacement in Concord of the native species by the Asian one must have occurred rapidly between 1950 and about 1970. MdsxFls: frequent => none. WorCo: uncommon declining (-0.400).

Ribes hirtellum: Decline due to purposeful extirpation to prevent pine blister rust. MdsxFls: occasional => occasional. WorCo: fairly common declining (-0.333).

10. DECLINING, LIKELY FOR REASONS OTHER THAN CLIMATE CHANGE AND/OR ONLY LOCALLY (16 species)

ACORUS CALAMUS (*Acorus americanus*, in error): Eaton (1974) lists this as very scarce when formerly common citing water pollution as the likely cause. MdsxFls: common => rare. WorCo: fairly common not declining (0.06).

Arethusa bulbosa: This was disappearing well before 1950. Fernald (1950) notes it as "rapidly becoming extinct .. s.[outh] of Nfld [Newfoundland] and Canada." Lamont & Young (2004) note the complete disappearance by 1940 of a population formerly growing in great abundance on Long Island, NY in 1877. MdsxFls: no records. WorCo: rare declining (-0.750).

Brasenia schreberi: Eaton (1974) indicates the decline in Concord is due to water pollution of the rivers: "Formerly common to abundant, now scarce except in unpolluted waters." MdsxFls: occasional => rare. WorCo: common increasing (0.333).

Calopogon tuberosus: Eaton (1974) notes: "progressive elimination of undisturbed habitat has reduced this formerly scarce orchid to the status of a rarity." MdsxFls: no records. WorCo: uncommon declining (-0.636).

Castilleja coccinea: Hosmer (1903) lists this only at Hayward's Swamp on the side of Annursnack Hill, the only place Thoreau found it. Primack et al. (2009) designating the Hosmer (1903) frequency of occurrence as "frequent" is based on misconstruing Hosmer's note (following his listing it only at Hayward Swamp), "Form with yellow bracts not uncommon.," as meaning not uncommon in Concord when in fact he means not uncommon within the population at Hayward's Swamp. Alfred Hosmer is the last person known to have seen this in Concord which was in 1902. Its disappearance from this last Concord site occurred well before any climate change effects. MdsxFls: no records. WorCo: presumed extirpated, last record in 1939, formerly sporadic. Now considered historical in Massachusetts.

Lupinus perennis (dry sandy banks, open gravelly places): Eaton (1974) lists this as scarce, becoming rare. MdsxFls: no records. WorCo: fairly common not declining (-0.152). On Massachusetts watch list.

Menyanthes trifoliata: Hosmer (1903) lists this as common. Pratt (1878) notes only two Concord locations and elsewhere not specified. Four Concord locations are noted in Thoreau's Journal. Eaton (1974) lists it as rare. Three locations where it formerly grew in Concord were ruined well before the 1970s. MdsxFls: no records. WorCo: uncommon not declining (-0.231).

Micranthes virginiensis (*Saxifraga virginiensis*): Pratt (1878) lists this as on rocks everywhere. Hosmer (1903) lists it as very common. Eaton (1974) lists it as infrequent. I found it in the 1980s to be scarce. Cherrie Corey (2014 pers. comm.) reports this still to be at the lime quarries in the Estabrook Woods and at Martha's Point in Concord. This species would be declining in metropolitan Boston due to disappearance of open rocky habitat. MdsxFls: common => rare. WorCo: fairly common not declining (0.055).

Platanthera orbiculata: Pratt (1878) records that he introduced this to Concord except for three plants he found, that he did not introduce. Most or all of the Hosmer (1903) report of this in Concord would be survivors of Minot Pratt's introduction. Thoreau's Journal and herbarium do not record him ever finding this in Concord. Eaton (1974) lists this as rare, status unknown. As this appears to have been disappearing by 1939 in Worcester County, the probable disappearance of only three native plants in Concord would have no relevance to climate change. MdsxFls: no records. WorCo: presumably extirpated, last record 1939. On Massachusetts watch list.

Platanthera psycodes: Pratt (1878) lists this as common in moist meadows. Hosmer (1903) calls it rather common, but then notes it at only two Concord localities (not in meadows) as if this was significant. Eaton (1974) lists it as uncommon, perhaps rare. The history of reference to it in Concord is consistent knowing that this orchid is a plant of river meadows and swampy open woods and that the Concord rivers (and their adjacent meadows) became polluted after Alfred Hosmer's time, particularly in the 1930s. Hosmer (1903) noted the two Concord locations because they were not by the rivers where the orchid was most plentiful. The three locations in the Estabrook Woods where I found it in the 1970s/80s include the only two specific locations cited by Hosmer. As I found that this plant occurs only in very small numbers where it does occur in the woods, it is not surprising that Primack et al. (2009) managed to find only one of the three locations. The evidence indicates decline in Concord, but most of it local (river pollution). MdsxFls: rare => rare. WorCo: fairly common declining (-0.394).

Pogonia ophioglossoides: Hosmer (1903) lists it as common. Pratt (1878) lists it as abundant. Eaton (1974) attributes the decline in this species due to destruction of its habitats (as he had observed it from the 1920s to the 1960s). MdsxFls: no records. WorCo: fairly common not declining (-0.167).

Prenanthes alba: MdsxFls: no records. WorCo: presumably extirpated, formerly uncommon, last record 1946.

Ranunculus aquatilis var. *diffusus* (*Ranunculus trichophyllus*): There are only three references to this in Thoreau's Journal, all from one site where he noted the plant new to him in 1854. Pratt (1878) lists it as common. Hosmer (1903) lists it from three Concord locales. Eaton (1974) lists it as uncommon. Experience of past Concord botanists is inconsistent. MdsxFls: rare => none. WorCo: none -- records there from eight townships with last record for it in 1946, presumed to be extirpated.

Rhododendron canadense: Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as occasional. The decline in this would be due largely to destruction/degradation of bogs in Concord and pollution of the river meadows in the early part of the 20th century as noted above for other species. MdsxFls: occasional => none. WorCo: fairly common not declining (-0.200).

ROSA RUBIGINOSA (*ROSA EGLANTERIA*): Pratt (1878) and Hosmer (1903) list this as common. The Middlesex County Flora (Dame & Collins 1888) lists this as occasional and not very common under each of its two previous names. Thus, it appears not to have been so popular outside of Concord. Eaton (1974) lists it as infrequent. I found it to be scarce in the 1970s/1980s. The decline in this escape from cultivation is most likely due to decline in its popularity as a yard shrub. MdsxFls: occasional => none. WorCo: rare declining (-0.83).

Silene caroliniana: A declining species, but declining well before 1950. Hosmer (1903) lists it as very common. Eaton (1974) lists it as occasional. MdsxFls: no records. WorCo: reports this perhaps extirpated in Worcester County with records from four townships the last being in 1932.

11. DECLINING FOR UNCERTAIN REASONS (20 species)

Anaphalis margaritacea (dry fields, clearings): Pratt (1878) lists this as abundant. Hosmer (1903) lists it as common. Eaton (1974) lists it as frequent. MdsxFls: frequent => occasional. WorCo: fairly common declining (-0.290).

Anemone virginiana (dry or rocky open woods): Eaton (1974) reports this uncommon, but widespread. MdsxFls: frequent => rare. WorCo: fairly common declining (-0.309).

ANTHEMIS COTULA (waste ground, roadsides): MdsxFls: occasional => none. WorCo: fairly common declining (-0.28).

Ceanothus americanus (dry open woods and thickets): Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists it as frequent. I found it occasional in the 1980s. MdsxFls: common => occasional. WorCo: fairly common declining (-0.255).

Chamerion angustifolium ("*Epilobium anagallidifolium*," in error) (recent clearings, recently burned woodlands, thickets): Eaton lists this as common. MdsxFls: common => none. WorCo: fairly common declining (-0.500).

Cirsium pumilum (dry open soil): Eaton (1974) says it is rare. MdsxFls: frequent => none. WorCo: uncommon declining (-0.514).

Corallorhiza maculata: Hosmer (1903) notes this from two Concord locations and states that it is not uncommon. Pratt (1878) does not list this at all. There are ten references (one of them outside Concord) to this in Thoreau's Journal with only three Concord localities noted. The historic record is somewhat consistent if Thoreau found three Concord stations, Pratt (1878) none and Hosmer (1903) two, with Hosmer's (1903) reference as "not uncommon" being to the greater Concord vicinity. Eaton (1974) lists it as scarce. This was never common or frequent in Concord. MdsxFls: occasional => none. WorCo: uncommon declining (-0.267).

Eurybia radula (bogs, sphagnous swamps and sphagnous shores): Eaton (1974) reports this as rare. On Massachusetts watch list. Endangered or protected in Kentucky, Maryland, New York, and elsewhere. MdsxFls: no records. WorCo: uncommon (-0.143, based on few records).

Gentianopsis crinita (brook meadows, ditch banks, wet thickets): Eaton (1974) lists this as occasional and transient. MdsxFls: rare (1897) => none. WorCo: fairly common declining (-0.368).

Geum rivale (wet peaty meadows and bogs): Although there are only four references to this in Thoreau's Journal, it is an apparently recently declining species. Eaton (1974) lists this as common. MdsxFls: occasional => none. WorCo: uncommon declining (-0.379).

Lysimachia hybrida (river meadows, swamps, shores): MdsxFls: no records. WorCo: uncommon declining (-0.615).

Moneses uniflora: Pratt (1878) and Thoreau never found this in Concord or in neighboring towns. Hosmer (1903) lists just two Concord locations for this. Eaton (1974) lists this as rare, at two locales different than those of Hosmer (1903). This scarce, hard-to-see species is a poor taxon to gauge frequency of occurrence as the historical record shows. MdsxFls: rare => none. WorCo: uncommon declining (-0.583).

Pedicularis canadensis (dry open woods and clearings): MdsxFls: frequent => rare. WorCo: uncommon declining (-0.696).

Polygala verticillata (dry or moist open sterile habitats): MdsxFls: no records. WorCo: fairly common (-0.273). On Massachusetts watch list.

Ranunculus flabellaris (streams, ponds): Pratt (1878) lists this as rather rare, in contrast to Hosmer (1903) (common), Eaton (1974) (rather common), and apparently Thoreau. MdsxFls: frequent => rare. WorCo: uncommon declining (-0.455).

Ranunculus flammula var. *ovalis* (shores): Pratt (1878) and Hosmer (1903) list this as common. Eaton (1974) lists this as uncommon. MdsxFls: no records. WorCo: no records. On the Massachusetts watch list.

Santcula marilandica (open commonly dry woods and thickets): MdsxFls: common => occasional. WorCo: fairly common declining (-0.280).

Spiranthes lacera var. *lacera* (fields, peaty meadows): MdsxFs: frequent => none. WorCo: uncommon declining (-0.677).

Thalictrum thalictroides (open woods usually in dry circumneutral soil): MdsxFls: frequent => rare. WorCo: fairly common declining (-0.263).

Viola pubescens (rich, usually deciduous woods): Hosmer (1903) lists this as rather common noting two localities in Concord. Pratt (1878) lists the area of the town it is found and one locality. Eaton (1974) lists it as rare. MdsxFls: rare => none. WorCo: fairly common declining (-0.362).

APPENDIX B
Listing by family of the 429 species used by Willis et al. (2008)

Species names are those used by Willis et al (2008) in an unpublished spreadsheet used for their work kindly provided by Willis Family names and the genera included under those families are those used in my online Concord flora (Angelo 2014b)

* - families cited by Willis et. al. (2008) as experiencing most loss
() - number of species in family
Integer beside each species is the amount of frequency change using frequency integers assigned by Willis et al. (2008) to Hosmer (1903) and to Primack et al. (2009) from data provided by the latter.

Species names in upper case are not native to Concord. Information in {} indicates origin of non-native species.

Non-native species =107, 43 species reported to be declining from data of Primack et al. (2009)
Native species = 322; 241 species reported to be declining from data of Primack et al. (2009)
Total species = 429, 284 species reported to be declining from data of Primack et al. (2009)

ACORACEAE (1)
Acorus americanus -3 {Concord species is *A. calamus* from Europe}

ADOXACEAE (5)
Sambucus nigra -1
Viburnum acerifolium 0
Viburnum lentago -2
Viburnum nudum 0
Viburnum recognitum 0

ALISMATACEAE (2)
Sagittaria latifolia -2
Sagittaria subulata -4

ANACARDIACEAE (5)
Rhus copallinum -1
Rhus glabra -1
Rhus typhina +1
Toxicodendron radicans -1
Toxicodendron vernix -1

APIACEAE (7)
Angelica atropurpurea -5
Cicuta bulbifera 0
Cicuta maculata -1
DAUCUS CAROTA -1 {from Eurasia}
PASTINACA SATIVA -2 {from Eurasia}
Sanicula marilandica -2
Sium suave -2

APOCYNACEAE (8)
Apocynum androsaemifolium -1
Apocynum cannabinum -5
Asclepias exaltata -3
Asclepias incarnata 0
Asclepias purpurascens -5
Asclepias syriaca -1
CYNANCHUM LOUISEAE +4 {from Europe}
VINCA MINOR +2 {from Eurasia}

AQUIFOLIACEAE (2)
Ilex mucronata 0
Ilex verticillata -2

ARACEAE (4)
Arisaema triphyllum -1
Calla palustris -1
Peltandra virginica 0
Symplocarpus foetidus 0

ARALIACEAE (2)
Aralia hispida -2
Aralia nudicaulis 0

ASTERACEAE* (59)
Achillea millefolium -1
Ambrosia artemisiifolia 0
Anaphalis margaritacea -2
Antennaria plantaginifolia -3
ANTHEMIS COTULA -3 {from Eurasia}
Bidens cernua -4
Bidens frondosa 0
CICHORIUM INTYBUS -1 {from Eurasia}
CIRSIUM ARVENSE -4 {from Eurasia}
Cirsium pumilum -5
CIRSIUM VULGARE -2 {from Eurasia}
Conyza canadensis -1
Doellingeria umbellata 0
Erechtites hieraciifolia -1
Erigeron annuus 0
Erigeron philadelphicus -1
Erigeron pulchellus -1
Eupatoriadelphus dubius 0
Eupatorium perfoliatum -2
Eurybia macrophylla -5
Eurybia radula -5
Gnaphalium uliginosum -2
Helianthus divaricatus -5
HIERACIUM AURANTIACUM +1 {from Europe}
Hieracium canadense -1
Hieracium paniculatum -1
Hieracium scabrum -2
Hieracium venosum -2
Ionactis linariifolius 0
Krigia virginica -1
Lactuca canadensis -1
Leontodon autumnalis -2
LEUCANTHEMUM VULGARE -1 {from Eurasia}
Mikania scandens 0
Oclemena acuminata -1
Packera aurea -3
Prenanthes alba -5
Prenanthes serpentaria -5
Pseudognaphalium obtusifolium 0

RUDBECKIA HIRTA -1 {from the Great Plains}
Sericocarpus asteroides -2
Sericocarpus linifolius -5
Solidago bicolor -2
Solidago caesia 0
Solidago canadensis 0
Solidago juncea 0
Solidago nemoralis -1
Solidago odora +2
Solidago rugosa 0
Solidago uliginosa -5
SONCHUS ASPER +3 {from Eurasia, Africa}
Symphyotrichum laeve -5
Symphyotrichum novaeangliae -3
Symphyotrichum patens -5
Symphyotrichum puniceum -2
Symphyotrichum undulatum -5
TANACETUM VULGARE -1 {from Eurasia}
TARAXACUM OFFICINALE -1 {from Eurasia}
Vernonia noveboracensis -3

BALSAMINACEAE* (1)
Impatiens capensis 0

BERBERIDACEAE (2)
BERBERIS VULGARIS -2 {from Eurasia}
PODOPHYLLUM PELTATUM +1 {from southern and midwestern US}

BORAGINACEAE (5)
ECHIUM VULGARE 0 {from Eurasia}
Myosotis arvensis +1
Myosotis laxa +1
MYOSOTIS SCORPIOIDES -1 {from Eurasia}
Myosotis verna -2

BRASSICACEAE (12)
ARMORACIA RUSTICANA -4 {from Europe}
BARBAREA VULGARIS 0 {from Eurasia}
CAPSELLA BURSAPASTORIS 0 {from Eurasia}
Cardamine bulbosa 0
CARDAMINE DIPHYLLA 0 {from western & northern New England}
Cardamine pensylvanica -2
CARDAMINE PRATENSIS +1 {from western New England & Eurasia}
DRABA VERNA +2 {from Eurasia}
LEPIDIUM CAMPESTRE +3 {from Eurasia}
Lepidium virginicum -1
RAPHANUS RAPHANISTRUM -1 {from Eurasia}
SISYMBRIUM OFFICINALE -2 {from Eurasia}

CABOMBACEAE (1)
Brasenia schreberi -2

CAMPANULACEAE* (7)
Campanula aparinoides -2
CAMPANULA RAPUNCULOIDES -1 {from Eurasia}
CAMPANULA ROTUNDIFOLIA -2 {from northern & western New England}
Lobelia cardinalis 0
Lobelia inflata -2
Lobelia spicata -5
Triodanis perfoliata -1

CAPRIFOLIACEAE (1)
Triosteum aurantiacum -1

CARYOPHYLLACEAE* (14)
CERASTIUM FONTANUM +4 {from Eurasia}
DIANTHUS ARMERIA 0 {from Eurasia}
Moehringia lateriflora 0
SAGINA PROCUMBENS +1 {from Eurasia}
SAPONARIA OFFICINALIS 0 {from Eurasia}
SCLERANTHUS ANNUUS -1 {from Eurasia}
Silene antirrhina -3
SILENE ARMERIA -5 {from Eurasia}
Silene caroliniana -3
SILENE VULGARIS +2 {from Eurasia}
SPERGULA ARVENSIS -2 {from Eurasia}
SPERGULARIA RUBRA -1 {from Eurasia}
STELLARIA GRAMINEA +1 {from Eurasia}
STELLARIA MEDIA -1 {from Eurasia}

CELASTRACEAE* (1)
Celastrus scandens -5

CHENOPODIACEAE (2)
CHENOPODIUM ALBUM 0 {from Eurasia}
Chenopodium simplex -5

CISTACEAE* (4)
Helianthemum canadense -1
Lechea intermedia -2
Lechea mucronata -5
Lechea tenuifolia -3

COMANDRACEAE (1)
Comandra umbellata -3

COMMELINACEAE (1)
Tradescantia virginiana 0

CONVOLVULACEAE (3)
Calystegia sepium -1
Cuscuta gronovii -1
IPOMOEA PURPUREA 0 {from the neotropics}

CORNACEAE* (4)
Cornus alternifolia -2
Cornus canadensis -1
Cornus racemosa -3
Cornus rugosa -3

CRASSULACEAE* (2)
HYLOTELEPHIUM TELEPHIOIDES -3 {the Concord species is *HYLOTELEPHIUM TELEPHIUM* from Eurasia}
Sedum acre +2 {from Eurasia}

CUCURBITACEAE (1)
ECHINOCYSTIS LOBATA +1 {from northern & western New England}

DIERVILLACEAE (1)
Diervilla lonicera -1

DROSERACEAE (2)
Drosera intermedia -2
Drosera rotundifolia +1

ERICACEAE* (25)
Andromeda polifolia -3
Chamaedaphne calyculata -1
Chimaphila maculata +1
Chimaphila umbellata -2
Epigaea repens -1
Eubotrys racemosa -3
Gaultheria procumbens -2
Gaylussacia baccata 0
Gaylussacia frondosa 0
Kalmia angustifolia 0
Kalmia latifolia -2
Kalmia polifolia -2
Lyonia ligustrina 0
Moneses uniflora -3
Monotropa hypopithys -2
Monotropa uniflora 0
Pyrola chlorantha -5
Pyrola elliptica 0
Rhododendron canadense -2
Rhododendron viscosum -1
Vaccinium angustifolium 0
Vaccinium corymbosum 0
Vaccinium macrocarpon -1

Vaccinium oxycoccus -4
Vaccinium pallidum 0

EUPHORBIACEAE* (3)
Acalypha rhomboidea -1
Chamaesyce nutans -6
EUPHORBIA CYPARISSIAS -1 {from Eurasia}

FABACEAE (23)
Amphicarpaea bracteata 0
Apios americana -2
Baptisia tinctoria -2
CHAMAECRISTA FASCICULATA +2 {from southeastern New England}
Crotalaria sagittalis -5
Desmodium nudiflorum -2
Desmodium paniculatum 0
Lespedeza capitata -1
Lespedeza frutescens +1
Lespedeza hirta -3
Lespedeza virginica -1
Lupinus perennis -5
MELILOTUS OFFICINALIS +2 {from Eurasia}
ROBINIA PSEUDOACACIA -1 {from central & southeastern US}
SECURIGERA VARIA +2 {from Eurasia}
Tephrosia virginiana -4
TRIFOLIUM ARVENSE 0 {from Eurasia, Africa}
TRIFOLIUM AUREUM 0 {from Eurasia}
TRIFOLIUM CAMPESTRE -2 {from Eurasia, Africa}
TRIFOLIUM HYBRIDUM 0 {from Eurasia}
TRIFOLIUM PRATENSE 0 {from Eurasia}
TRIFOLIUM REPENS 0 {from Eurasia}
VICIA CRACCA 0 {from Eurasia}

GENTIANACEAE (2)
Gentiana andrewsii -5
Gentianopsis crinita -5

GERANIACEAE (2)
Geranium maculatum -1
GERANIUM ROBERTIANUM 0 {from central, western & northern New England}

GROSSULARIACEAE* (2)
Ribes hirtellum -5
RIBES RUBRUM -4 {from Europe}

HALORAGACEAE* (1)
Proserpinaca palustris -3

HAMAMELIDACEAE* (1)
Hamamelis virginiana -1

HYPERICACAE* (4)
Hypericum canadense -2
Hypericum gentianoides -3
HYPERICUM PERFORATUM -1 {from Eurasia}
Triadenum virginicum -2

IRIDACEAE (4)
Iris prismatica -3
IRIS PSEUDACORUS +1 {from Eurasia}
Iris versicolor -1
Sisyrinchium angustifolium -1

LAMIACEAE* (18)
GALEOPSIS TETRAHIT 0 {from Europe}
GLECHOMA HEDERACEA 0 {from Eurasia}
Hedeoma pulegioides -5
LEONURUS CARDIACA -2 {from Eurasia}
Lycopus americanus -2
Lycopus virginicus -1
MENTHA ARVENSIS -3 {from Eurasia}
MENTHA PIPERITA -5 {hybrid with parents from Eurasia, Africa}
MONARDA BRADBURIANA -5 {from the Midwest & southern US, not known in Concord}
MONARDA MEDIA -3 {from the Midwest & southern US }
NEPETA CATARIA -3 {from Eurasia}
Prunella vulgaris -2
Pycnanthemum incanum -5
Pycnanthemum muticum -5
Scutellaria galericulata -1
Scutellaria lateriflora 0
THYMUS PULEGIOIDES 0 {from Europe}
Trichostema dichotomum -1

LAURACEAE (2)
Lindera benzoin +2
Sassafras albidum -2

LENTIBULARIACEAE* (5)
Utricularia cornuta -4
Utricularia gibba -2
Utricularia inflata -5
Utricularia macrorhiza -1
Utricularia purpurea -4

LILIACEAE* (19)
Allium canadense -2
ASPARAGUS OFFICINALIS -4 {from Eurasia}
Clintonia borealis -5
CONVALLARIA MAJALIS 0 {from Eurasia}
HEMEROCALLIS FULVA +1 {from Asia}
Hypoxis hirsuta -2

Lilium canadense -4
LILIUM LANCIFOLIUM -3 {from Asia}
Lilium philadelphicum -5
Maianthemum canadense +1
Maianthemum racemosum -1
Medeola virginiana 0
ORNITHOGALUM UMBELLATUM +1 {from Eurasia}
POLYGONATUM BIFLORUM 0 {from southwestern New England}
Polygonatum pubescens -2
Trillium cernuum -4
Trillium undulatum -3
Uvularia sessilifolia -1
Veratrum viride -3

LYTHRACEAE (2)
Decodon verticillatus +1
LYTHRUM SALICARIA +2 {from Eurasia}

MALVACEAE (2)
Hibiscus moscheutos -1
MALVA NEGLECTA -2 {from Eurasia}

MELASTOMATACEAE (1)
Rhexia virginica -1

MENYANTHACEAE (2)
Menyanthes trifoliata -5
Nymphoides cordata -3

MOLLUGINACEAE (1)
Mollugo verticillata -1

MYRICACEAE (3)
Comptonia peregrina -2
Morella pensylvanica -1
Myrica gale -5

MYRSINACEAE* (6)
ANAGALLIS ARVENSIS -5 {from Eurasia}
Lysimachia hybrida -2
LYSIMACHIA NUMMULARIA +2 {from Eurasia}
Lysimachia quadrifolia 0
Lysimachia thyrsiflora -1
Trientalis borealis -1

NELUMBONACEAE (1)
NELUMBO LUTEA 0 {from Connecticut southward}

ONAGRACEAE* (8)
Circaea alpina -2

Circaea lutetiana 0
Epilobium anagallidifolium -5
Epilobium coloratum -2
Ludwigia alternifolia 0
Ludwigia palustris -2
Oenothera biennis -1
Oenothera perennis -3

ORCHIDACEAE* (14)
Arethusa bulbosa -5
Calopogon tuberosus -5
Corallorhiza maculata -5
Cypripedium acaule 0
Goodyera pubescens -2
Goodyera tesselata -5
Platanthera clavellata -5
Platanthera grandiflora -2
Platanthera lacera 0
Platanthera orbiculata -4
Platanthera psycodes -4
Pogonia ophioglossoides -3
Spiranthes cernua -4
Spiranthes lacera -5

OROBANCHACEAE* (7)
Agalinis paupercula -1
Aureolaria flava -2
Aureolaria pedicularia -2
Castilleja coccinea -4
Melampyrum lineare -1
Orobanche uniflora 0
Pedicularis canadensis -5

OXALIDACEAE* (1)
Oxalis stricta -1

PAPAVERACEAE (3)
CHELIDONIUM MAJUS 0 {from Eurasia}
Corydalis sempervirens -1
Sanguinaria canadensis +1

PENTHORACEAE* (1)
Penthorum sedoides -4

PHRYMACEAE* (1)
Mimulus ringens -1

PHYTOLACCACEAE (1)
Phytolacca americana 0

PLANTAGINACEAE (11)
Chelone glabra -1
Gratiola aurea -4
LINARIA VULGARIS 0 {from Eurasia}
Nuttallanthus canadensis -1
PLANTAGO ARISTATA +1 {from central US}
PLANTAGO LANCEOLATA 0 {from Eurasia}
PLANTAGO MAJOR 0 {from Eurasia}
VERONICA OFFICINALIS 0 {from Eurasia}
Veronica peregrina 0
Veronica scutellata -2
VERONICA SERPYLLIFOLIA 0 {from Eurasia}

POLYGALACEAE (3)
Polygala paucifolia -2
Polygala sanguinea -2
Polygala verticillata -5

POLYGONACEAE (17)
FAGOPYRUM ESCULENTUM -4 {from cultivation, originally from Asia}
Polygonella articulata +1
Polygonum arifolium +1
POLYGONUM AVICULARE 0 {probably from Eurasia}
POLYGONUM CUSPIDATUM +3 {from Asia}
POLYGONUM HYDROPIPER +1 {from Eurasia, Australia}
Polygonum hydropiperoides 0
Polygonum lapathifolium +2
POLYGONUM ORIENTALE -3 {from Asia, Australia}
Polygonum pensylvanicum +3
POLYGONUM PERSICARIA 0 {from Asia}
Polygonum punctatum -4
Polygonum sagittatum -2
RUMEX ACETOSELLA 0 {from Eurasia}
RUMEX CRISPUS 0 {from Eurasia}
RUMEX OBTUSIFOLIUS -1 {from Eurasia}
Rumex orbiculatus -4

PONTEDERIACEAE (1)
Pontederia cordata 0

PORTULACACEAE (2)
CLAYTONIA VIRGINICA +1 {from western Massachusetts, Connecticut}
PORTULACA OLERACEA -3 {probably from Eurasia}

RANUNCULACEAE* (18)
Actaea pachypoda 0
Anemone quinquefolia -2
Anemone virginiana -5
Aquilegia canadensis -1
AQUILEGIA VULGARIS +1 {from Europe}

Caltha palustris -1
Clematis virginica -4
Coptis trifolia 0
Ranunculus abortivus -1
RANUNCULUS ACRIS -1 {from Eurasia}
RANUNCULUS BULBOSUS 0 {from Eurasia}
Ranunculus flabellaris -5
Ranunculus flammula -5
Ranunculus trichophyllus -4
Thalictrum dioicum -1
Thalictrum pubescens -1
Thalictrum thalictroides -2
XANTHORHIZA SIMPLICISSIMA 0 {from mid-Atlantic to southeastern US}

RHAMNACEAE (1)
Ceanothus americanus -2

ROSACEAE* (19)
Agrimonia gryposepala -2
Amelanchier canadense 0
Fragaria virginiana -1
Geum aleppicum -5
Geum canadense -1
Geum rivale -5
Photinia melanocarpa -1
POTENTILLA ARGENTEA 0 {from Eurasia}
Potentilla canadensis 0
Potentilla norvegica 0
POTENTILLA RECTA +3 {from Eurasia}
Prunus americana 0
Prunus serotina 0
Prunus virginiana -2
Rosa carolina -3
ROSA EGLANTERIA -5 {from Eurasia}
Rosa virginiana -2
Spiraea alba -1
Spiraea tomentosa -2

RUBIACEAE* (7)
Cephalanthus occidentalis 0
Galium asprellum 0
Galium circaezans 0
Galium trifidum -5
Galium triflorum 0
Houstonia caerulea -3
Mitchella repens -3

SAPINDACEAE (1)
Acer pensylvanicum +1

SARRACENIACEAE* (1)
Sarracenia purpurea -3

SAXIFRAGACEAE* (3)
Chrysosplenium americanum -2
Saxifraga pensylvanica -6
Saxifraga virginiensis -3

SCROPHULARIACEAE (1)
VERBASCUM THAPSUS 0 {from Eurasia}

SMILACACEAE* (2)
Smilax herbacea -2
Smilax rotundifolia 0

SOLANACEAE (1)
SOLANUM DULCAMARA 0 {from Eurasia}

SPARGANIACEAE (1)
Spargantum eurycarpum -2

URTICACEAE (2)
Boehmeria cylindrica -1
Urtica dioica -5

VERBENACEAE (2)
Verbena hastata -1
Verbena urticifolia -2

VIOLACEAE* (7)
Viola blanda -5
Viola cucullata 0
Viola labradorica -5
Viola lanceolata 0
Viola pedata -1
Viola pubescens -2
Viola sororia 0

VITACEAE (3)
Ampelopsis brevipedunculata (*Parthenocissus quinquefolia* intended & thus duplicated) -1
Parthenocissus quinquefolia -1
Vitis labrusca 0

XYRIDACEAE (1)
Xyris torta -1

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AJO PEAK TO TINAJAS ALTAS: FLORA OF SOUTHWESTERN ARIZONA PART 8. EUDICOTS: ACANTHACEAE – APOCYNACEAE

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ABSTRACT

A floristic account is provided for seven eudicot families as part of the vascular plant flora of the contiguous protected areas of Organ Pipe Cactus National Monument, Cabeza Prieta National Wildlife Refuge, and the Tinajas Altas Region in southwestern Arizona: Acanthaceae (5 genera, 7 species), Adoxaceae (1 genus, 1 species), Aizoaceae (2 genera, 3 species), Amaranthaceae (12 genera, 22 species), Anacardiaceae (1 genus, 2 species), Apiaceae (6 genera, 6 species), and Apocynaceae (5 genera, 10 species). This is the eighth contribution for this flora published in Phytoneuron and also posted open access on the website of the University of Arizona Herbarium (ARIZ).

This contribution to our flora in southwestern Arizona is the eighth published in a series in Phytoneuron and also posted open access on the website of the University of Arizona Herbarium (ARIZ; Figure 1). Seven eudicot families are included in this contribution: Acanthaceae (5 genera, 7 species), Adoxaceae (1 genus, 1 species), Aizoaceae (2 genera, 3 species), Amaranthaceae (12 genera, 22 species), Anacardiaceae (1 genus, 2 species), Apiaceae (6 genera, 6 species), and Apocynaceae (5 genera, 10 species).

The first article in this series includes maps and brief descriptions of the physical, biological, ecological, floristic, and deep history of the flora area (Felger et al. 2013a). This flora includes the modern, present-day taxa as well as fossil records from packrat middens. Explanation of the format for the flora series is provided in part 3 (Felger et al. 2013b). These contributions are also posted open access on the website of the University of Arizona Herbarium (ARIZ). Family designations follow APG III (Angiosperm Phylogeny Group 2009; also see Stevens 2001). Vernacular, or common names, when known or deemed worthwhile, are given in English, Spanish, and the Hia-Ced O'odham dialect, respectively. Fossil specimens are indicated with a dagger symbol (†) and taxa represented by fossils no longer present in the flora are marked with two dagger symbols (††). All specimens cited are at the University of Arizona Herbarium (ARIZ) unless otherwise indicated by the

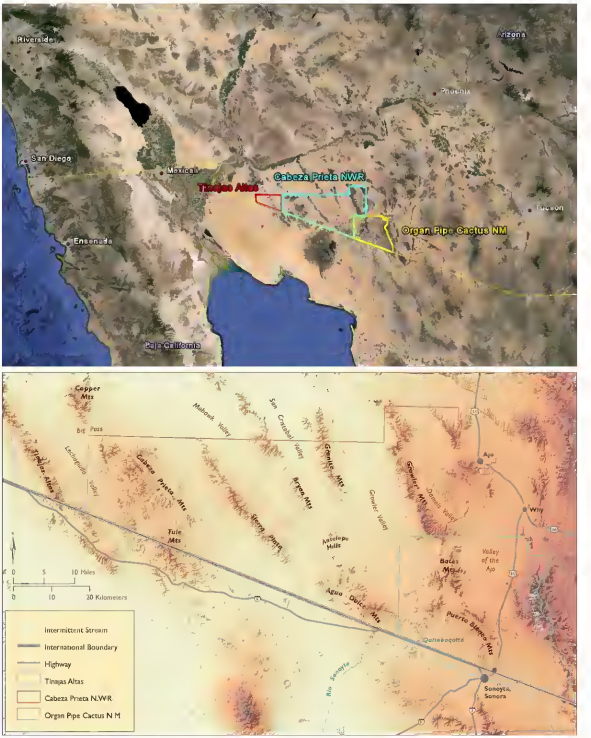

Figure 1. Flora area in southwestern Arizona. (A) Above, overview of regional context, (B) below, detail with local place names. Map B prepared by Ami Pate of Organ Pipe Cactus NM, 2013.

abbreviations for herbaria at Cabeza Prieta National Wildlife Refuge (CAB), Organ Pipe Cactus National Monument (ORPI), and the standardized abbreviations for herbaria (Index Herbariorum, Thiers 2013). All photos and scans are by Sue Rutman unless otherwise stated and all botanical illustrations are by Lucretia Brezeale Hamilton (1908–1986). Descriptions and keys pertain to taxa and populations within the flora area.

ACANTHACEAE – Acanthus Family

Herbaceous perennials and shrubs (also some trees in other regions, such as black mangrove, *Avicennia germinans*). Leaves opposite, simple, entire; stipules none. Flowers attractive, subtended by bracts; corollas bilaterally symmetrical. Stamen 2, or 4 in *Ruellia*. Fruit a capsule, elastically and explosively dehiscent with seeds borne on retinacula (distinctive hooks); seeds 4, or 10 or more in *Ruellia*.

Acanths have their greatest diversity in tropical and subtropical regions. In the flora area they are generally winter dormant or cease growing during the cooler times of year and during drought. The five genera and seven species in the flora area all occur in Organ Pipe. *Carlowrightia* and *Justicia californica* extend into Cabeza Prieta and only *J. californica* makes it to the hyperarid Tinajas Altas Region in the westernmost part of flora area. *Carlowrightia arizonica* and *Justicia californica* are the most arid-inhabiting members of the family in the Southwest and the only ones extending into California. Major factors limiting acanth distributions in the region seem to be freezing weather and the paucity of summer rains.

Hummingbirds are the usual pollinators of the red- or orange-flowered species of *Anisacanthus* and *Justicia*, generally called *chuparrosa* in Mexico. These flowers are diurnal and open all day, or the corollas may fall away with daytime heat. The pure white flowers of *J. longii* are nocturnal, and the others acanths have whitish to lavender corollas opening shortly after sunrise and falling with daytime heat.

Worldwide, mostly in tropics and subtropics, few in temperate regions; at least 220 genera and 4000 species. About 35 species occur in the Río May region of southeastern Sonora and southwestern Chihuahua (Martin et al. 1998) and the numbers diminish to the north and westward (Daniel 1984; Felger 2000).

1. Shrubs, often to 1 m or more tall; corollas red or orange.

   2. Bark shredding; stamens positioned along the lower lip of the corolla, the anthers opening toward the upper lip. ..... **Anisacanthus**
   2. Bark not shredding; stamens positioned along the upper lip of the corolla, the anthers opening toward the lower lip. ..... **Justicia californica, J. candicans**

1. Herbaceous to subshrub (suffrutescent) perennials, mostly less than 1 m tall; corollas white, cream, blue, violet, or purple.

   3. Stems 6-ridged (hexagonal in cross-section); flowers and fruits enclosed by a pair of heart-shaped to nearly triangular or kidney-shaped bracts 7–15 mm long; corollas twisted through 180°, pink to pale violet with white markings on lip. ..... **Dicliptera**
   3. Stems 4-ridged (quadrate) to rounded (terete) in cross-section; flowers and fruits not enclosed by bracts as above; corollas not twisted, white, white and lavender, or violet colored.

4. Corollas white with lavender and yellow markings on the lip; fruits narrowed at the base, abruptly flared above. ..... **Carlowrightia**
4. Flowers pure white or lavender; fruits not noticeably narrowed at the base, and not flared above.

5. Petioles to 0.7 cm long, the leaf blades 0.5–7 cm long; flowers axillary, paired and subsessile, white, and nocturnal; fertile stamens 2; seeds 4. ..... **Justicia longii**
5. Petioles to 5 cm long, the leaf blades mostly 5–15 cm long; flowers in terminal, panicle-like inflorescences, the flowers usually pedicelled, lavender, and diurnal; fertile stamens 4; seeds 10 or more. ..... **Ruellia**

Anisacanthus thurberi (Torrey) A. Gray
Desert honeysuckle. Figure 2.

Shrubs with relatively slender stems and peeling bark; generally becoming leafless during winter or extended drought. Corollas orange-red (brick orange), 4–5 cm long. Stamens 2. Capsules 1–1.5 cm long, seeds 4 or fewer. Flowering non-seasonally although usually winter dormant.

Organ Pipe except the southwestern portion; mostly along canyon bottoms, and washes in hills and mountains, and sometimes abundant in washes of the valley floor.

Arizona, New Mexico, and northwestern mainland Mexico.

OP: Alamo Canyon, *Nichol 4 May 1939*. Bates Well, 18 Nov 1939, *Harbison 26156*. Estes Canyon, 2500 ft, 4 Nov 1978, *Bowers 1240*. 0.5 mi E of Lukeville, 11 Nov 1987, *Felger 87-317*.

Carlowrightia arizonica A. Gray
Lemilla. Figure 3.

Suffrutescent perennials or subshrubs with slender, delicate, brittle stems. Leaves drought deciduous, sessile to petioled, 0.6 (dry seasons)–5 (hot, wet weather) cm long; blades mostly lanceolate. Corollas about 1 cm wide, white with a yellow "eye" and purple nectar guidelines on the upper lip. Stamens 2. Flowering primarily late spring and during summer rainy season. The flowers open around sunrise, and the corollas and attached stamens fall as a unit with daytime heat. Capsules ca. 1 cm long, conspicuously narrowed at base (stipitate), flared and ovate- to cordate-discoid (latterly flattened) above, and glabrous. Seeds 4, ovate- to cordate-discoid, 3 mm wide, the surfaces conspicuously papillose.

Mostly on rocky slopes, but not the hottest, driest places, and sometimes along gravelly washes. Widespread in Organ Pipe and much of Cabeza Prieta. In open places it is frequently grazed by rabbits, rodents, and especially chuckwallas, which sometimes reduce the plant to a mass of short, stubby stems.

Southern Arizona to west Texas, widespread in Sonora, both states of Baja California, disjunct in Anza-Borrego in San Diego County, California, and through Mexico to Costa Rica. The geographic range essentially spans that of the entire genus. It is a "taxonomically complex species with numerous diverse morphological forms" (Daniel 1984: 167).

OP: Alamo Canyon, *Nichol 4 May 1939*. Estes Canyon, 9 May 1979, *Bowers 1695*. 0.5 mi N of Visitor Center, 16 Apr 1985, *Van Devender 85-110*. Quitobaquito Hills, 6 Apr 1988, *Felger 88-266*.
CP: Cabeza Prieta Tanks, 6 Apr 1979, *Lehto L23542* (ASU). Canyon at Agua Dulce Tank, and at Eagle Tank, 13 & 15 Jun 1992, *Felger* (observations).

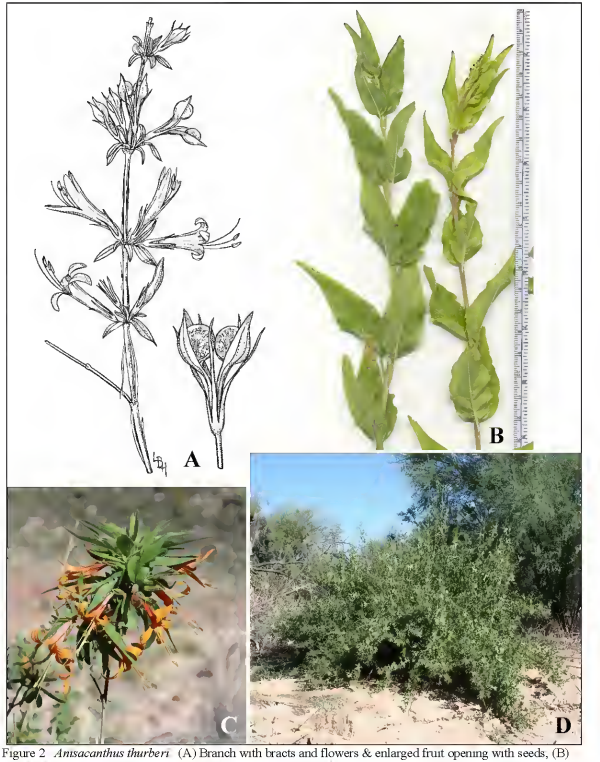

Figure 2. *Anisacanthus thurberi*. (A) Branch with bracts and flowers & enlarged fruit opening with seeds, (B) Cherioni Wash near Hwy 85, 25 Aug 2008, (C) Bull Pasture Trail, Ajo Mts, 27 Feb 2014, (D) Kuakatch Wash, W of Hwy 86, 7 Oct 2006.

Figure 3 *Carlowrightia arizonica* (A) Flower, Bumblebee, Yavapai Co., photo by Max Licher; (B) Alamo Canyon, 7 Sep 2013

Dicliptera resupinata (Vahl) de Jussieu
Fold-wing; *alfalfilla*. Figure 4.

Herbaceous perennials, often bushy, and also flowering in the first season or year. Flowers enclosed by a pair of conspicuous, usually heart-shaped to nearly triangular or kidney-shaped bracts 7–15 mm long, these held on the plant long after the flowering season and sometimes becoming white. Corollas about 1–2 cm long, twisted through 180 degrees, pink or pale violet with white markings on the lip; flowering at various seasons; mostly winter dormant. Stamens 2. Capsules 4 mm long, obovoid, with 4 seeds.

Canyons in the Ajo and Diablo Mountains including Alamo, Arch, Diablo, and Estes Canyons, and high grassy slopes in the Ajo Mountains.

Western Mexico including Baja California Sur, Arizona and New Mexico.

OP: Alamo Canyon, *Nichol 4 May 1939*. Canyon Diablo, 15 Apr 1951, *Supernaugh 453*. Arch Canyon, 3500 ft, 28 Mar 1965, *Lockwood 163*. Near cliff overhanging Arch Canyon Trail, Ajo Mts, 2947 ft., 26 Oct 2003, *Rutman 20031026-23*.

Figure 4 *Dicliptera resupinata* (A) Garden in Ajo, 29 Sep 2013; (B) above the arch, Arch Canyon, 12 Sep 2013

Justicia

Herbaceous perennials and shrubs. Flowers variously tubular. Stamens 2. Capsules with 4 or fewer seeds. This genus, mostly subtropical and tropical of about 700 species worldwide, is polyphyletic and the largest genus in the family. The New World species with closely related small genera of about 400 species are monophyletic (Kiel et al. 2013; McDade et al. 2000, McDade & Kiel 2006).

1. Herbaceous to suffrutescent perennials; flowers white, nocturnal ..... **Justicia longii**
1. Shrubs; flowers red or red-orange, diurnal.

2. Stems bluish green for several seasons, generally sparsely leafy to essentially leafless, densely covered with microscopic hairs 0.05–0.1 mm long; corollas red-orange, capsules 16–22 mm long, pubescent ..... **Justicia californica**
2. Stems brown after the first season, leafy, with hairs 0.2–1 mm long; corollas red with white markings on the lower lip; capsules 10–14 mm long, glabrous ..... **Justicia candicans**

Justicia californica (Bentham) D.N. Gibson
[*Beloperone californica* Bentham]
Desert hummingbird bush, *chuparrosa*, wipisimal. Figure 5.

Sprawling to mound-shaped shrubs often 1–2+ m tall. Stems loosely interlacing, pale bluish green, densely pubescent with minute hairs. Often leafless or nearly so much of the year or with sparse foliage, leaves highly variable, 2–8 cm long, quickly drought deciduous, petioled, the blades mostly ovate to orbicular, often moderately thick. Corollas red-orange, 2.5–4 cm long, tubular and flaring above. Capsules 1.5–2 cm long, club-shaped, and pubescent. Seeds 4, rounded, 3–3.3 mm diameter, and glabrous. Flowering October to May with sufficient soil moisture and warm weather, often with massive flowering in February and March. As with various other desert acanths, the capsules tend to open with morning heat.

Widespread and common across the flora area, especially at lower elevations along dry watercourses and sometimes on bedrock slopes. This species is one of the more important hummingbird plants in the region and a favorite food of desert bighorn. Mornings during spring flowering often become hummingbird battlefields, especially along gravelly watercourses with palo verde (*Parkinsonia florida*), desert lavender (*Hyptis*), and ironwood (*Olneya*). The flowers attract Costa's, Rufous, and Allen's hummingbirds, as well as honeybees and butterflies. *Chuparrosa*, derived from *chupar* 'to suck', is used in Mexico for various hummingbird-adapted flowers (see Felger & Moser 1985). Carpenter bees (*Xylocopa*) and sometimes hummingbirds slit the floral tube and rob (consume) nectar, apparently without providing pollination (Maloof & Inouye 2000). Sweet nectar can be sucked from the flower base, mostly in spring, as a minor snack or trail food (Bean & Saubel 1972; Felger & Moser 1985).

Baja California Sur and northwestern Sinaloa northward to southeastern California and southwestern Arizona.

OP: Diablo Canyon, 21 Mar 1935, *Peebles 10825*. Alamo Canyon, *Nichol 26 Mar 1939*. Rancho Bonito, 2 Dec 1939, *Harbison 26208* (SD). Arch Canyon, 3500 ft, 28 Mar 1965, *Lockwood 153*. Senita Basin, along a wash, 6 Dec 1978, *Hodgson H205* (DES).

CP: Tule Tank, 24 Nov 1934, *Goodding 2074*. Papago Well, 15 Apr 1941, *Benson 10787*. Agua Dulce Pass, 19 Mar 1987, *Elias 10213*. Heart Tank, 27 Feb 1993, *Felger 93-165*.

TA: Tinajas Altas, 26 Mar 1932, *Shreve 5940*. SW side of Tinajas Altas range, bajada at granitic hills, 10 Jan 2002, *Felger* (observation).

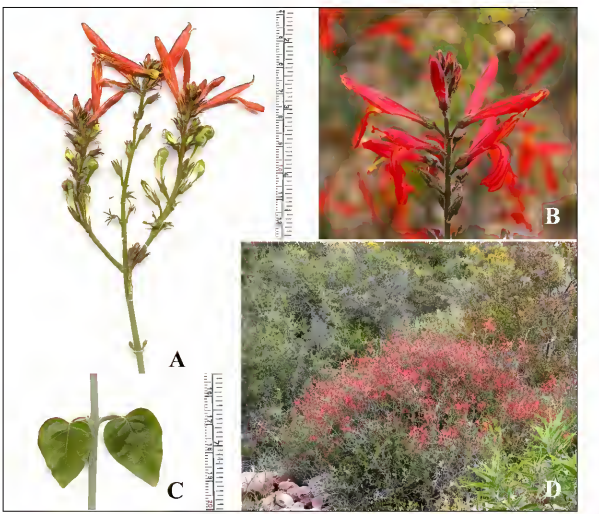

Figure 5. *Justicia californica*. (A & C) Garden in Ajo, 10 Feb 2009; (B) Estes Canyon Trail, 5 Feb 2006; (D) southern end of Sauceda Mts, along Pipeline Road, BLM, 18 Mar 2005.

Justicia candicans (Nees) L.D. Benson
[*Jacobinia ovata* A. Gray]
Chuparrosa. Figure 6.

Shrubs often 1–1.5 m tall, with slender, brittle, and leafy stems. Leaves gradually drought deciduous, 1.5–5+ cm long, petioled, the blades ovate and thin. Corollas often 2.5–3.5 cm long, bright red, with a slender tube and flared above with white markings on the lower lip. Capsules 10–15 mm long, glabrous. Seeds flattened, 3–4 mm diameter, and glabrous. Potentially flowering with sufficient soil moisture and warm weather, except during the summer rainy season when the plants produce vegetative growth; massive flowering often in February and March.

Canyon bottoms, often as an understory shrub, and rocky, north–facing slopes in the Ajo Mountains. It has been in the Ajo Mountains for at least 1200 years.

Southern Arizona to Oaxaca, and Baja California Sur.

OP: Pitahaya Canyon, *Nichol 23 Feb 1939*. Alamo Canyon, 13 Dec 1939, *Harbison 26250*. Puerto Blanco Drive, 22 Oct 1964, *Ranzoni 363* (ORPI). †Alamo Canyon, fruits, seeds, 1150 ybp.

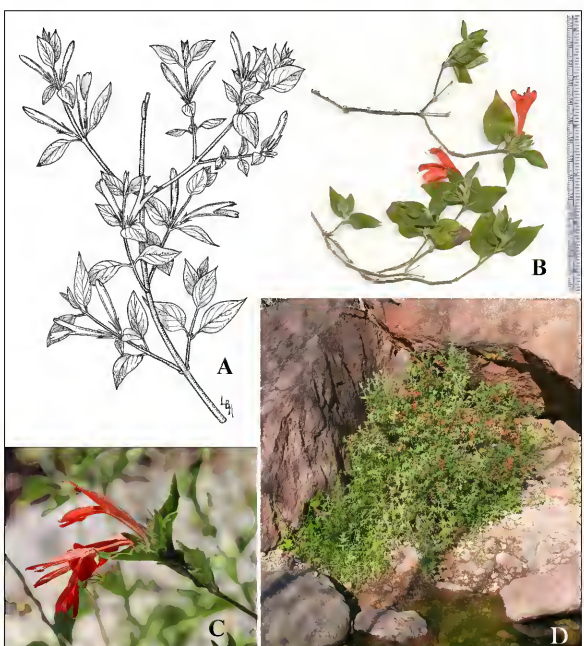

Figure 6. *Justicia candicans*. (A) Flowering branch. Alamo Canyon: (B) 24 Mar 2008; (C) 17 Oct 2013; (D) 12 Mar 2005.

Justicia longii Hilsenbeck
[*Siphonoglossa longiflora* (Torrey) A. Gray]
Long-flower tube-tongue. Figure 7.

Herbaceous perennials from a hard, knotty, and slightly woody base and short-rhizomatous rootstocks. Leaves and smaller stems drought deciduous. Leaves often 1–7 cm long, subsessile to petioled, the blades narrowly lanceolate (in winter) to elliptic or ovate (in summer). Flowers clustered in axils and surrounded by firm, persistent bracts. Flowers nocturnal, opening in the early evening; corollas and attached stamens falling shortly after dawn; corollas 3.5+ cm long, pure white with a prominent, slender tube. Capsules 6.5–10 mm long. Seeds flattened, 2+ mm diameter, tuberculate. Flowering during spring and summer. The plants are often severely grazed by wildlife. The flowers, like those of other *Justicia*, are not fragrant.

Rocky and gravelly soils, canyons and slopes, especially north-facing. Documented for the Puerto Blanco and Ajo Mountains and other scattered localities in Arizona Uplands in Organ Pipe.

Southern Arizona and west Texas, and Sonora north of the Guaymas region. Sphinx moths, the presumed pollinators, have been observed feeding at the flowers (Hilsenbeck 1990).

OP: Above Dripping Springs, 16 Apr 1952, *Parker 9753*. Estes Canyon, *Warren 9 May 1975*. Walls Well Rd, *Van Devender 30 Aug 1978*. Bull Pasture, 2700 ft, 9 May 1979, *Bowers 1693*. Arch Canyon, 11 Mar 1983, *Daniel 2590* (ASU).

Ruellia nudiflora (Engelmann & A. Gray) Urban
[*R. nudiflora* var. *runyonii* (Tharp & F.A. Barkley) B.L. Turner]
Violet Ruellia. Figure 8.

Herbaceous perennials from rhizomatous rootstocks; winter dormant. Leaves often 5–17 cm long, petioled, the blades ovate to broadly ovate. Inflorescences terminal, paniculate, openly branched with slender branchlets. Flowers showy, the corollas violet-purple, 3–5 cm wide, only moderately bilaterally symmetric; warmer months. Stamens 4. The flowers open near sunrise and the corollas with their attached stamens fall away with daytime heat, often about midday or early afternoon. Capsules firm and ellipsoid, about 1–2 cm long, usually with 10 or more seeds; opening explosively. This species also produces cleistogamous flowers (self-fertilizing flowers forming fruits without the flowers opening) near the base of the plants, especially early in the growing season or at times of stress.

Locally in the eastern and northern portions of Organ Pipe. Often in shady places including canyon bottoms to high elevations in the Ajo Mountains, and mesquite bosques such as Dos Lomitas and Armenta Ranch and other low-lying habitats with clayish or silty soils. The flowers are visited by bees.

Arizona and Texas to Mississippi, and Mexico to Costa Rica.

This species has been called "violet wild petunia," an unfortunate name because *Petunia* is a genus in the potato family (Solanaceae). The showy flowers and winter hardiness make *Ruellia* a favorite in native plant gardens in southern Arizona.

OP: 2 mi SE of Walls Well, near N end of Ajo Mts, abundant along sandy wash, 30 Aug 1945, *Haskell 3215*. Canyon Diablo, 15 Apr 1951, *Supernaugh 431* (ORPI). Ajo Mts, 20 Aug 1952, *Fouts 431*. Arch Canyon, 3500 ft, 28 Mar 1965, *Lockwood 163*. Armenta Well, *Wirt 10 Aug 1990* (ORPI). Dos Lomitas, *Rutman 16 Aug 2001* (ORPI).

Figure 7 *Justicia longii* (A) Bull Pasture Trail, 31 Mar 2008, (B & D) Ajo Mt Drive near Wild Horse Tanks, Diablo Mts, 14 Sep 2013, (C) Estes Canyon, 30 Jan 2014.

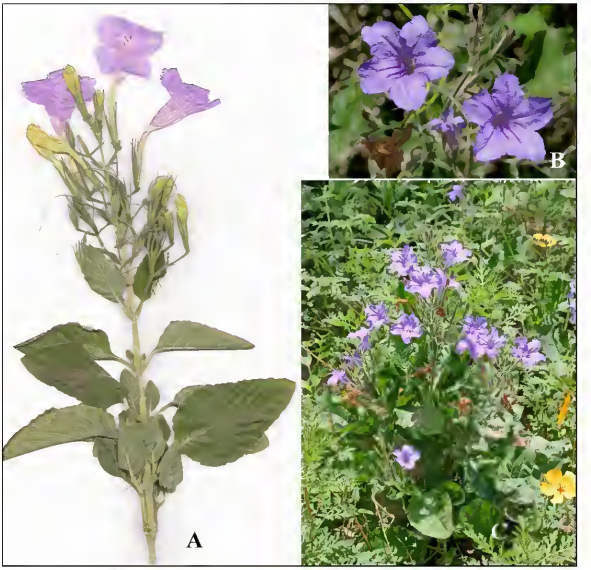

Figure 8. *Ruellia nudiflora*. Ditch along Hwy 86 east of Why. (A) 22 Sep 2008, (B & C) 16 Aug 2006.

ADOXACEAE – Adoxa Family

****Sambucus cerulea** Rafinesque

[*S. nigra* Linnaeus subsp. *cerulea* (Rafinesque) Bolli. *S. mexicana* C. Presl ex de Candolle. *S. cerulea* var. *mexicana* (C. Presl ex de Candolle) L.D. Benson. *S. neomexicana* Wooton. *S. cerulea* var. *neomexicana* (Wooton) Rehder]

Blue elderberry, *tápiro*. Figure 9.

Small trees with thick trunks and limbs, the wood soft and weak, the stems pithy. Leaves deciduous in summer; new growth and leaves appear in fall and winter. Flowers cream white in dense, often flat-topped inflorescences (cymes), flowering mostly winter and spring. Fruits berry-like, about 5 mm in diameter, dark purplish to black.

The one record in the flora area might have been a tree planted at the former ranch in Alamo Canyon. Elderberry trees often were planted at ranches and towns in southern Arizona and northern Sonora, largely for the berries, which are mostly made into preserves, jelly, and wine, and also used for medicinal purposes. It served Hia-Ced O'odham people "as a medicine and sometimes for food" (Betty Melvin in Zepeda 1985: 65). The unripe fruits and herbage can be poisonous.

Blue elderberry is probably native to the Sonoran Desert Region but at elevations above the desert. *Sambucus cerulea* occurs in western North America including northwestern Mexico. Eriksson and Donoghue (1997: 567) report that "our accessions of *Sambucus nigra* sensu Bolli (1994) form a clade with the exception of *S. cerulea*, which we conclude should be treated as a separate species."

The genus includes about 10 species in the Old and New World, mostly temperate and subtropical or montane in the topics. The fruits have been used as a source of blue or black dye, especially by the Romans. Pan was said to dye his hair using elderberries.

OP Alamo Canyon, *Tinkham Apr 1942*.

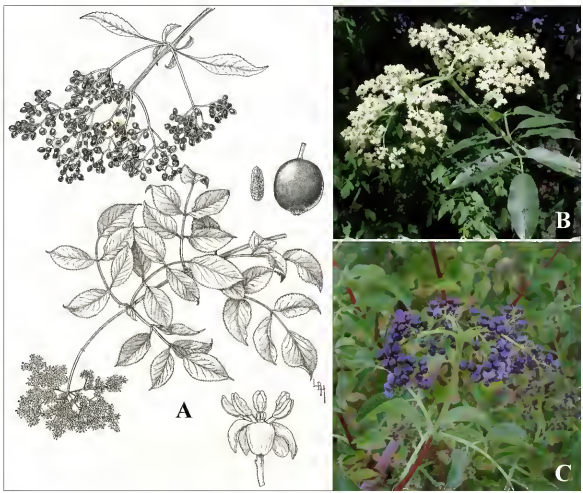

Figure 9. *Sambucus coerulea*. (A) By LBH. (B) Oak Creek Canyon, Coconino Co.; (C) Sedona, Coconino Co. Photos by Max Licher (SEINET).

AIZOACEAE – Aizoon Family

Low-growing and generally weedy annuals in the flora area. Leaves opposite (those in the flora area). Flowers radial. Sepals mostly 5. Petals none but numerous petal-like linear staminodes (modified stamens) often present. Fruits of capsules.

1. Winter-spring annuals; plants extremely succulent; flowers white with numerous slender petal-like staminodes; capsules opening at the top. ..... **Mesembryanthemum**
1. Summer-fall annuals; plants not succulent or sometimes semi-succulent; flowers pinkish, the calyx 5-lobed, staminodes none; capsules opening around the middle ..... **Trianthema**

*Mesembryanthemum

Iceplant; *hielitos*

Plants extremely succulent. Flowers with numerous, slender, petal-like staminodes; fertile stamens many. Fruits at first fleshy, becoming dry capsules with valves at the flattened top opening when moist.

Two species of this South African genus are naturalized in portions of the Sonoran Desert where they occur as winter-spring annuals. Both species were first found in Organ Pipe in spring, 1995, an El Niño year with copious spring rains. They became locally established on hypersaline soil, straddling the U.S.–Mexico border and were more widespread and abundant on the Mexico side, especially along Mexico Highway 2. These species are occasionally seen elsewhere in southern Arizona and are especially common in sandy soils around Puerto Peñasco in northwestern Sonora. Both species are extensively naturalized along the Pacific Coast of the Californias and South America, and other Mediterranean regions including southern Australia.

1. Leaves with a thick but broad blade, and an evident petiole.... **Mesembryanthemum crystallinum**
1. Leaves cylindrical, sessile (petiole and blade not distinguishable)
..... **Mesembryanthemum nodiflorum**

*Mesembryanthemum crystallinum Linnaeus

[*Cryophytum crystallinum* (Linnaeus) N.E. Brown. *Gasoul crystallinum* (Linnaeus) Rothmaler]

Crystal iceplant; *hielitos*. Figure 10.

Plants spectacularly fleshy, the surfaces covered with large, watery, crystal-like vesicles. Leaves often 2–10 cm long, narrowed basally or with a petiole; blades usually obovate to broadly spatulate, or somewhat triangular. Flowers ca. 1 cm wide with white staminodes. Capsules ca. 1 cm wide, rounded like a clenched fist when dry, quickly gaping open by slit-shaped valves when wet (even on years-old dry specimens) to reveal the seeds and closing again when dry. Seeds 1 mm in diameter and numerous.

Locally abundant on saline soils along the international border in the south central to southwestern part of Organ Pipe.

Native of southern Africa. It has been in southern Arizona since the early 20th century and at Puerto Peñasco and elsewhere in northwestern Sonora at least since the 1970s (Felger 2000; Felger & Wilder 2012).

OP: La Abra Plain, near International Boundary Monument 170, *Rutman 11 May 1995*.

Figure 10. *Mesembryanthemum crystallinum*. All images from the Rio Sonoyta floodplain near international boundary, Sonora, 28 Mar 2013.

***Mesembryanthemum nodiflorum** Linnaeus
Slender-leaf iceplant; *helitos*. Figure 11.

The plants turn bright red with heat and drying conditions. Leaves slender, more or less terete, and extremely succulent. Flowers ca. 5 mm wide, the staminodes white, becoming yellow as the flower fades. Capsules obovoid, ca. 5 mm wide, seeds brown, 0.7–0.8 mm in diameter, numerous. No herbivory has been noted, despite the plants' succulence.

Southwestern margin of Organ Pipe on saline soils, from La Abra Plain to Hocker Well and Corner Well and the adjacent southeastern corner of Cabeza Prieta, and adjacent northwestern Sonora. The population southward from the southwest corner of Organ Pipe extended as far as the eye could see—covering hundreds if not thousands of acres, much of it not disturbed.

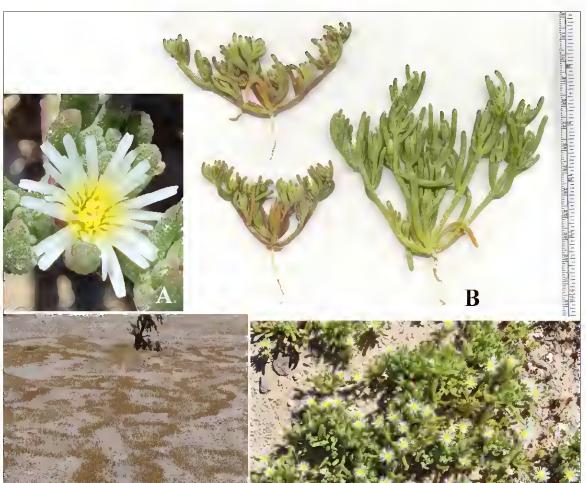

Figure 11. *Mesembryanthemum nodiflorum*. (A & D) International boundary near El Huerfano, Sonora, 5 Mar 2014, (B) La Abra Plain, 19 Mar 2008, (C) near SW corner of Organ Pipe, 23 Jul 2008.

Native to southern Africa. In the New World naturalized along the Pacific Coast of the Californias and South America. First recorded in Arizona in the early 1980s (8 mi N of Maricopa, *Hamilton 17 Mar 1983*).

OP: La Abra Plain, probably more than 10,000 plants, near International Boundary Monument 170, *Rutman 11 May 1995*. S boundary from Hocker Well to Corner Well, 11 May 1995, *Rutman*, photos.
CP: Near Corner Well, 11 May 1995, *Rutman* (observation).

Trianthema portulacastrum Linnaeus
Horse purslane, *verdolaga de cochi*, kasvañ. Figure 12.

Hot-weather ephemerals, often reddish, sometimes semi-succulent. Stems often 15–60 cm long. Leaves 3–4.5 (9) cm long on robust, young plants, the older plants with smaller and usually thicker leaves, leaf blades obovate to orbicular, stipules and expanded leaf bases forming a membranous sheath around the stem. Flowers small, sessile and solitary in leaf axils, partially enclosed by the sheathing leaf base; calyx petal-like, 5-lobed, the lobes 2.3–12.5 mm long, pink with

a green horn. Capsules circumscissile, the base corky, and the "lid" or "cap" truncate or more often 2-horned, retaining 1 or 2 seeds. Capsules several-seeded; seeds about 7 in number, and 2 mm long. The seeds disperse three ways: 1 or 2 seeds disperse with the capsule cap, and the others remain with the basal part of the capsule and dribble away or remain with the capsule attached to the mother plant.

Figure 12. *Trianthema portulacastrum*. (A) Plant with enlarged fruit, flower, and seed; (B) near Qutobaquito, 11 Sep 2008; (C) near Qutobaquito, 20 Aug 2006; (D) Gila River near Gillespie Dam, 31 Mar 2013.

Temporarily moist places at lower elevations, especially in hypersaline soils; disturbed habitats, washes, low places, and alkaline flats. The specimen records are from the southern margin of flora area, perhaps as a result of dispersal from disturbed habitats in nearby Sonora.

Horse purslane is widespread across the Sonoran Desert even in remote, natural habitats (Felger & Wilder 2012). Widely distributed and often weedy in the Americas. Some authors propose that it may be introduced from the Old World in post-Columbian times. It ranges across large areas of the Old World and is a serious agricultural weed worldwide (e.g., Holm et al. 1997).

Two forms are evident in the flora area and elsewhere in the Sonoran Desert (Felger 2000): a robust form, with larger leaves and flowers, and a more common form with smaller leaves and flowers. Both occur intermixed, and intermediate forms appear to be absent. Perhaps related to the two Sonoran Desert forms are two biotypes well known in India, the red, or *rubra*, form and the green, or *flava* form (e.g., Mohammed & Sen 1990).

OP: Williams Spring, *Van Devender 30 Aug 1978*. 0.5 mi W of Lukeville, 10 Nov 1987, *Felger 87-284*. Aguajita 14 Sep 1988, *Felger 88-430* (larger-flowered morph), *88-431* (smaller-flowered morph).
CP: Adobe Well (Simmons 1966).

AMARANTHACEAE – Amaranth Family (includes Chenopodiaceae)

Annuals to woody shrubs. Leaves alternate or opposite, simple, often entire; stipules none. Flowers small and mostly inconspicuous, bisexual or unisexual; sepals (tepals) usually 4 or 5, often dry and membranaceous; petals none. Fruits 1-seeded.

1. Shrubs, obviously woody (borderline cases will key both ways).

2. Leaves flat, or at least broader than thick; twigs not succulent, often woody; flowers unisexual, the female flowers and/or fruits winged. ..... **Atriplex**
2. Leaves succulent, rounded in cross section but the upper surface often somewhat flattened, about as thick as wide; twigs semi-succulent, not woody and not spinescent; flowers bisexual, the female flowers and fruits not winged. ..... **Suaeda**

1. Plants herbaceous or only slightly woody at base.

3. At least some leaves opposite or appearing opposite (some leaves may be alternate or appear to be 3's in *Tidestromia*); flowers bisexual.

4. Plants with branched hairs; leaves with conspicuous petioles, the blades generally about as wide as long, broadly ovate to obovate-orbicular……**Tidestromia**
4. Plants glabrous or with simple hairs; leaves sessile or short-petioled, more than twice as long as wide, linear to elliptic or oblanceolate.

5. Annuals, not succulent, with simple hairs or sometimes glabrate with age; leaves narrowly elliptic or oblanceolate to oblong……**Gomphrena**
5. Perennials, markedly succulent and glabrous; leaves linear…….. **Nitrophila**

3. Leaves alternate; flowers unisexual or bisexual.

6. Winter-spring annuals; leaves hastate lanceolate-linear (at least the lower, larger leaves); flowers with 1 stamen and 1 sepal. …… **Monolepis**
6. Spring or summer annuals; leaves not hastate lanceolate-linear; stamens and sepals more than 1.

7. Female flowers and fruits enclosed in 2 sepal-like bracts. ..... **Atriplex**
7. Female flowers and fruits not enclosed in sepal-like bracts or the bracts.

8. Leaves and younger stems with soft, white hairs; fruiting calyx lobes hooked at tips. ..... **Bassia**
8. Plants glabrous, glaucous, or mealy but lacking slender white hairs; calyx lobes not hooked.

9. Leaves sessile or subsessile, narrowly linear or scale-like. .....**Salsola**
9. Leaves petioled, the blade expanded and much wider than petioles.

10. Flowers unisexual..... **Amaranthus**
10. Flowers bisexual.

11. Plants not stinky; leaves dark green to red-green and shiny on both surfaces, or sometimes grayish below; seed margins acute (thin) with a distinct "rim"; seed surface dull even after removal of pericarp. .... **Chenopodiastrum**
11. Plants stinky, even when dry; leaves pale-colored and mealy on both surfaces; seed margins obtuse (broad); seed surface shiny blackish after removal of pericarp. ..... **Chenopodium**

Amaranthus

Annuals with a well-developed taproot. Leaves alternate, petioled. Flowers small and unisexual. Fruits small, indehiscent utricles or circumscissile (splitting around the middle) capsules. Seeds lens-shaped and compressed, erect in the fruit, smooth, red-brown to blackish (usually white or light colored among domesticated grain amaranths that probably were grown in the flora area in prehistoric times; Felger 2007; Rea 1997).

Five amaranths occur in the flora area, although only *A. fimbriatus* and *A. palmeri* are common and widespread. These two species tend to produce a single main stem. *Amaranthus palmeri* has female and male flowers on separate plants (dioecious). The others produce both female and male flowers on the same plant (monoecious), and the male flowers generally fall away soon after the pollen is shed. Among *A. albus* and *A. crassipes* the apical meristem is often not dominant, resulting in the lateral branches being as large or larger than the main axis. In *A. ×tucsonensis* the branching habit may be somewhat intermediate. *Amaranthus crassipes* has indehiscent fruits, and the others have dehiscent, circumscissile capsules (the fruit separates at a "line" around the middle and the top falls away like a miniature cap).

1. Stems erect, ascending, procumbent or prostrate; inflorescence branches and pedicels often thickened and moderately to strongly wavy (sinuous) and/or corky; fruits dehiscent or not, rough or sculptured at least towards the tip.

2. Peduncles markedly thickened and corky, forming an unique compact, hard knotty structure at the base of the plant and smaller clusters form in the leaf axils; fruits indehiscent. .....**Amaranthus crassipes**
2. Peduncles not conspicuously corky as above; fruits dehiscent (capsules).

3. Bracts beneath (subtending) flowers often spine-tipped and conspicuously longer than the flower; female flowers with 3 sepals. ..... **Amaranthus albus**
3. Bracts usually not spine-tipped and usually shorter than, or as long as the flower; female flowers with 5 sepals. .....**A. ×tucsonensis**

1. Stems usually erect or ascending, the plants often robust; inflorescence branches and pedicels mostly straight (the inflorescence branch tips often drooping), not thickened and corky; fruits dehiscent (circumscissile), smooth-surfaced.

4. Male and female flowers on the same plant; inflorescences "soft," the bracts not spiny or firm; female sepals conspicuously fringed; stamens 3. .....**Amaranthus fimbriatus**
4. Male and female flowers on different plants; inflorescence bracts (not sepals) firm and often sharp; female sepals not fringed; stamens 5. .....**Amaranthus palmeri**

***Amaranthus albus** Linnaeus
[*A. graecizans* of authors, not Linnaeus]
Pigweed, tumbleweed pigweed. Figure 13.

Robust, weedy plants, to ca. 80 cm tall, at maturity sometimes becoming tumbleweeds. Stems often yellowish. Female flowers with 3 sepals and dehiscent fruits. Male flowers with 3 stamens. Fruits of dehiscent, circumscissile capsules.

Common in urban and agricultural areas just south of Organ Pipe in the Sonoyta region and occasionally spreading into the border region of Organ Pipe east of Lukeville (Felger 1990, 2000). The 1939 record from the Ajo Mountains was the only record until 2013, when it was found in abundance in several miles of Alamo Canyon after the major flood of September 2012 (Rutman, 2 Nov 2013, photos).

Widespread and weedy in many parts of the world, in the New World from Alaska and Canada to South America; probably native to tropical parts of North America. Plants in southern Arizona and northern Sonora are probably var. *pubescens* (Uline & W.L. Bray) Fernald, distinguished by being sticky (viscid-pubescent, the hairs glandular) and having crisped leaf margins.

OP. Ajo Mts, *Harbison 13 Dec 1939* (SD)
Sonora. Ejido Morelia, ca. 8 km W of Sonoyta and 0.5 km N of Río Sonoyta (1.5 mi by road S of MEX Hwy 2), common weed, to 80 cm, 11 Nov 1987, *Felger 87-306*.

Amaranthus crassipes Schlechtendal var. **crassipes**
Spreading amaranth. Figure 14.

Plants highly variable in size, but mostly less than 20–30 cm across. Stems often semi-succulent, especially on larger plants, mostly prostrate, or sometimes turning upward at the tip (procumbent) or the central stem erect. Female flowers with 5 sepals. Male flowers with 3 stamens. Fruits indehiscent.

Wet clayish or silty soils of playas, wash banks, and dirt tanks in at least four places in the western part of the flora area following favorable summer or early fall rains. The population in Las Playas is extensive and the plants are often browsed, probably by rabbits.

Figure 13. *Amaranthus albus*. Alamo Canyon: (A & B) 2 Nov 2013; (C & D) 2 Nov 2013

Figure 14. *Amaranthus crassipes*. San Cristobal Wash at Camino del Diablo, 26 Sep 2013.

Variety *crassipes* occurs in southeastern United States, West Indies, northern South America, and southern and eastern Mexico, and is disjunct (native?) in northwestern Sonora and southwestern Arizona where it is known from relatively few localities. Another variety occurs in Texas, Coahuila, and Chihuahua.

OP: Old field, Armenta Well Ranch, 13 Sep 1978, *Bowers 1531* (ORPI).
CP: Jose Juan Tank, wet mud, 14 Sep 1992, *Felger 92-713*. Las Playas, 28 Nov 2001, *Felger 01-547*. San Cristobal Wash, where Camino del Diablo/Bates Road crosses the wash, *Rutman 26 Sep 2013*.
TA: Coyote Water, 25 Oct 2004, *Felger 04-24*.

Amaranthus fimbriatus (Torrey) Bentham ex S. Watson
Fringed amaranth, *bledo*, *quelitillo*, cuhukkia i vakĭ. Figure 15.

Summer-fall annuals, less than 1 m tall, the plants sometimes persisting until the first frost of late fall or winter; glabrous, pale green or often reddish especially late in the season. Leaves narrowly lanceolate. Inflorescences bracts and sepals herbaceous, not prickly. Female and male flowers on the same plant. Female flowers green and white, urn-shaped, the sepals 5 and fringed (fimbriate, rarely essentially entire). Stamens 3. Fruits of dehiscent, circumscissile capsules. Seeds 0.85–1 mm wide, lens-shaped, red-brown to blackish.

Common and widespread, especially at lower elevations, often on sandy soils, washes and valley plains, dunes, bajadas, floodplains, roadsides, and sometimes on rocky slopes. Widespread in the flora area for at least 32,000 years.

Sinaloa and Baja California Sur to southwestern United States

Figure 15. *Amaranthus fimbriatus*. (A) Plant, branch, female flower, and seed; (B) Kuakatch Wash near Hwy 85, 8 Sep 2006

OP: Bates Well, *Harbison 19 Nov 1939*. (SD) S of Estes Canyon, 12 Sep 1978, *Bowers 1520*. Aguajita Wash, 14 Sep 1988, *Felger 88-416* †Alamo Canyon, fruits, seeds, 1150 to 32,000 ybp (3 samples) †Montezuma's Head, fruits, seeds, 13,500 to 21,840 ybp (3 samples).

CP: Daniels Arroyo at Charlie Bell Road crossing, 18 Aug 1992, *Felger 92-663*. Bates Well Road at E boundary of Refuge, 14 Sep 1992, *Felger 92-679* (CAB). Pinacate Lava, 15 Sep 1992, *Felger 92-772*. Pinta Sands, 1 Feb 1992, *Felger* (observation).

TA: Tinajas Altas, 26 Oct 2003, *Felger* (observation). Coyote Water, 25 Oct 2004, *Felger 04-25* †Butler Mts, fruits, seeds, 8160 ybp.

Amaranthus palmeri S. Watson

Careless weed, pigweed, *quelite de las aguas*, cuhugia. Figure 16.

Well-watered plants reaching 1–1 6+ m tall, otherwise mostly smaller, sometimes only 5–10 cm tall, glabrous or essentially so. Terminal inflorescences commonly drooping near the tip (except young or very small plants), female and male flowers on separate plants. Female plants with spinescent bracts and sepals, the sepals 5. Stamens 5. Fruits of dehiscent, circumscissile capsules. Seeds 1 mm wide, lens-shaped, red-brown to blackish.

Common and widespread, and seasonally abundant, roadsides and other disturbed areas, washes and arroyo bottoms, dirt tanks (*charcos*), and valley bottoms, and sometimes even on rocky slopes. It has been in the Ajo Mountains for at least 1200 years.

Southwestern United States and much of Mexico; weedy and adventive worldwide.

This abundant, often robust summer annual was a major food plant across much of the Sonoran Desert. Young or half-grown plants were consumed as greens (Betty Melvin in Zepeda

1985: 56), and the small, black seeds of mature plants were parched and ground. Fresh plants were sometimes baked in coals or cooked and rolled "into a ball and baked on hot coals; this could be stored for future use" (Castetter & Bell 1951: 201). The seeds, seed-bearing branches, or entire plants were often stored. Betty Melvin said, "we would cook it. Yes that's the plant you have to wash and wash to get all the dirt out and then you boil it, you boil the little leaves until they are tender and then you refry it with some onions and it's very good. If you mix it with some cheese it's even better" (Zepeda 1985: 56).

OP: Bates Well, *Harbison 19 Nov 1939* (SD). Dos Lomitas, *Warren 17 Nov 1974*. S of Estes Canyon, 12 Sep 1978, *Bowers 1521*. Aguajita Wash, 14 Sep 1988, *Felger 88-441*. †Alamo Canyon, stems, fruits, seeds, 1150 ybp.

CP: Pinacate lava flow, 22 Mar 1992, *Harlan 110* (CAB). O'Neill's Grave, 11 Apr 1992, *Harlan 183* (CAB). Daniels Arroyo at Charlie Bell Rd, 18 Aug 1992, *Felger 92-665*. San Cristobal Wash, 14 Sep 1992, *Felger 92-688*.

TA: No records but expected at least along Coyote Wash.

Figure 16. *Amaranthus palmeri*. (A) Plant, branch, female flower (below), male flower (above), and seed, (B), male flowers, Hwy 85 roadside, mile 20 between Ajo and Gila Bend, 6 Sep 2013; (C) Alamo Canyon, 15 Sep 2013; (D) Growler Canyon, Bates Mts, 9 Sep 2012.

Amaranthus ×tucsonensis Henrickson
Tucson amaranth Figure 17

Plants often bright pink, generally erect, often with a main axis but also often with well-developed lateral branches. Flower clusters axillary and also with many small, crowded clusters in the terminal axis, but the terminal flowering stem or inflorescence not drooping (as often seen in *A. palmeri*); flower clusters and flowers not spinescent. Bracts beneath (subtending) female flowers mostly shorter than, to about as long as the sepals. Female and male flowers on the same plant. Female flowers with 5 sepals, the sepals relatively broad although moderately narrowed at the base but not narrowly clawed, the sepals at first rather erect and with age spreading or reflexed. Male flowers with 5 stamens. Fruits of dehiscent, circumscissile capsules.

The Organ Pipe collections are from Ajo Mountain canyons and Armenta Well Ranch. The collection history spans more than six decades. It is common or abundant on north-facing slopes above Bull Pasture and probably elsewhere in similar situations in the Ajos, where it is usually found with the wild tepary, *Phaseolus acutifolius*.

Tucson amaranth is seldom common and is known from only a few widely scattered localities in southern Arizona (near Tucson and in Organ Pipe) and in southeastern Sonora (Henrickson 1999). This enigmatic amaranth may be of hybrid origin as proposed by Henrickson (1999) or if not a stabilized hybrid then perhaps a variety of *A. retroflexus* Linnaeus (Costea et al. 2001; also see Mosyakin & Robertson 2003).

The plants might be confused with *A. albus* or *A. palmeri*. The 5 female sepals and 5 rather than 3 stamens readily distinguish *A. ×tucsonensis* from *A. albus*. *Amaranthus ×tucsonensis* is distinguished from *A. palmeri* by its shorter, non-spinescent bracts and non-spiny female sepals, shape of the female sepals, roughened fruit "cap" or "lid," and the continuous terminal inflorescence is not drooping as in *A. palmeri*.

OP. Alamo Canyon, 13 Dec 1939, *Harbison 26249*. Bull Pasture, *Wirt 29 Oct 1989*. Arch Canyon, N-facing slope below the arch, 900 m, 2 Dec 1990, *Felger 90-560*. Above Bull Pasture, trail to Mt. Ajo, 1030 m, 22 Oct 2006, *Rutman 20061022-13*.

Figure 17. *Amaranthus ×tucsonensis*. Bull Pasture Trail above Bull Pasture, 22 Oct 2006.

††?**Amaranthus** sp./spp.

Several fossil collections may represent more than one species.

OP: Alamo Canyon, fruit, 1150 ybp. Montezuma's Head, fruits, 13,500 & 20,490 ybp [The 13,500 ybp specimen may be *A. ×tucsonensis*]. Puerto Blanco Mts, seeds, 980 & 990 ybp.

TA: Tinajas Altas, seeds, 9900 & 10,600 ybp.

Atriplex – Saltbush

Annuals to woody shrubs. The plants scurfy gray or whitish due to inflated hairs that collapse upon drying. Leaves mostly alternate, the lowermost ones sometimes opposite. Flowers unisexual; male and female flowers on the same or separate plants. Female flowers and fruits enclosed in a pair of sepal-like bracts; as the fruits develop the bracts enlarge, thicken, and often grow various ornamentations such as wings and crests.

Seeds of some *Atriplex* species were parched or cooked with other foods but generally served as emergency food (Hodgson 2001). Young plants of herbaceous species or young shoots of shrubs were cooked as greens or with other foods for the salty flavor (Rea 1997).

1. Annuals; male and female flowers on the same plant.

   2. Fruiting bracts disk-shaped (orbicular), evenly toothed all around the margin... **Atriplex elegans**
   2. Fruiting bracts widest above middle, more or less truncate with coarse teeth arising above the middle. ..... **Atriplex pacifica**

1. Woody shrubs; male and female flowers on separate plants (except *A. lentiformis*)

   3. Fruiting bracts 4-winged (4 wing-like margins).

      4. Larger shrubs, commonly 1 m or more in tall; larger leaves often more than 3 cm long, 4–6 (8) mm wide; mature fruits with bracts often 1–2 cm long. ..... **Atriplex canescens**
      4. Smaller shrubs, commonly 1 m or less in height; larger leaves often 1–3 (4+) cm long, 2–4 mm wide; mature fruits with bracts often 0.4–0.5 (0.8) cm long. ..... **Atriplex linearis**

   3. Fruiting bracts not winged, the margins toothed or not.

      5. Bracts not toothed, or the teeth shallow and much broader than long; leaves mostly more than three cm long, the petioles well developed; male and female flowers on the same plant ..... **Atriplex lentiformis**
      5. Bracts conspicuously toothed, teeth 7 or more and mostly longer than wide; leaves mostly less than 2 cm long, sessile to subsessile; male and female flowers on separate plants. ..... **Atriplex polycarpa**

Atriplex canescens (Pursh) Nuttall

Four-wing saltbush; *chamizo cenizo*; 'onk 'i:vakĭ. Figure 18.

Shrubs to 2 m tall with scurfy gray-green herbage, tardily drought deciduous. Flowering in spring and summer. Leaves scurfy gray-green, entire, narrowly spatulate to narrowly oblong, larger leaves reaching 3–4.5 (5) × (0.2) 0.4–0.8 cm. Male and female flowers on separate plants. Fruiting bracts conspicuously 4-winged, often 1–2 cm diameter.

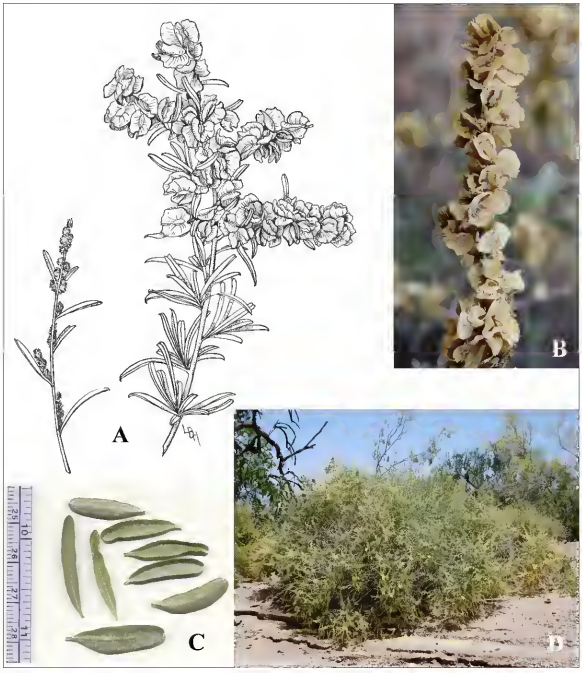

Figure 18. *Atriplex canescens* subsp. *canescens*. (A) Staminate (left) and pistillate branches, (B) fruiting bracts, Estes Canyon, 20 Jan 2014, (C) Kuakatch Wash near Hwy 85, 29 Jan 2014, (D) Kuakatch Wash near Hwy 85, 23 May 2010.

Wash margins and xeroriparian areas of valley bottoms and sometimes on rocky slopes to high elevations. It grew in the Ajo Mountains 9600 years ago.

A polymorphic species; western North America and northern Mexico.

Tea made from the leaves was taken as an emetic by the Seris (Felger & Moser 1985). Livestock favor this species due to its high protein content. Populations on Organ Pipe are probably still recovering since livestock were removed in the late 1970s.

OP: Tres Alamos Canyon, *Nichol 24 Feb 1939*. Wash NE of Pinkley Peak, 32 Oct 2003, *Rutman 20031031-1* (ORPI). †Alamo Canyon, leaves, fruit, 9570 ybp.
CP: Pinta Sands, *Simmons 17 Oct 1962* (CAB). Little Tule Tank, *Simmons 19 May 1963*. Packrat Hill, 25 Feb 1993, *Felger 93-61*. Charlie Bell Rd, 1 km W of Refuge boundary, 5 Mar 1994, *Felger 94-24*.

††**Atriplex confertifolia** (Torrey & Frémont) S. Watson
Shadscale

Low, subshrubs. Shadscale occurred in Ice Age woodlands in the Ajo Mountains but seems to have been fairly scarce. Today it is a dominant element in the Great Basin Desert in saline valley bottoms above the Mogollon Rim. The nearest present-day population is in the vicinity of Safford and Thatcher in Graham County, Arizona, near the margin of the Sonoran Desert.

Oregon and California to North Dakota and Chihuahua.

OP: Montezuma's Head, leaves, fruit, 13,500 & 21,840 ybp.

Atriplex elegans (Moquin-Tandon) D. Dietrich
[*A. elegans* subsp. *fasciculata* (S. Watson) H.M. Hall & Clements. *A. fasciculata* S. Watson]
Wheelscale orach; *chamizo cenizo*; 'onk 'i:vakĭ. Figure 19.

Annuals or short-lived perennials, with scurfy gray-green herbage, maturing from May through October. Leaves 0.8–3 (4.7) cm long, mostly oblong to oblanceolate. Male and female flowers on the same plant. Fruiting bracts disk- or wheel-shaped (as reflected in the English common name), 2.4–5 mm wide, compressed, orbicular, the margins crenulate to toothed throughout, the teeth small to large and coarse.

Gravelly, sandy soils of dry riverbeds and larger washes and floodplains, and margins of larger playas, often on alkaline/saline soils, and disturbed, weedy habitats including roadsides. Widely scattered localities in the flora area and in the Ajo Mountains 9600 years ago. The young plants were eaten as greens or used as seasoning by the Gila River Pimas (Rea 1997; Russell 1908).

Widespread in Arizona; southeastern California to western Texas, Baja California, and Sonora to Chihuahua and Durango.

The two subspecies are of doubtful significance and often grow intermixed, such as at Alamo Canyon and Quitobaquito (Felger 2000). Subsp. *elegans* is characterized by having thinner leaves, the lower leaves with wavy and often toothed margins, the upper leaves often entire, and the fruiting bracts coarsely toothed. Subsp. *fasciculata* is characterized by having generally thicker leaves with entire margins, and crenulate to shallowly small-toothed fruiting bracts. Younger and more robust plants tend to resemble subsp. *fasciculata*, whereas older and perhaps more water-stressed plants tend to key to subsp. *elegans*. The variation seems continuous, apparently sometimes changing between early- and late-season growths. The subspecies show some geographic segregation but with a very broad region of overlap. Subsp. *elegans* reported for Durango, Chihuahua, and western Texas to

Arizona, southeastern California, and northern Sonora southward to the vicinity of Guaymas. Subsp. *fasciculata* known from southern California, northern Baja California, northwestern Sonora, and southern Arizona.

OP: Quitobaquito *Nichol 28 Apr 1939*, 23 Jul 1986, *Felger 86-207*. Ajo Mt Drive, 2000 ft, 5 Nov 1977, *Bowers 912*. Alamo Canyon, *Van Devender 31 Aug 1978* (ORPI). NNW of Lukeville, *Rutman 14 Mar 1995* (ORPI). Armenta Ranch, old fields, 1 Feb 2002, *Felger 02-74*. †Alamo Canyon, fruits, 9570 ybp.

CP: Tule Well, 13 Apr 1992, *Harlan 253* (CAB). Dos Playas, 13 Jun 1992, *Felger 92-581*.

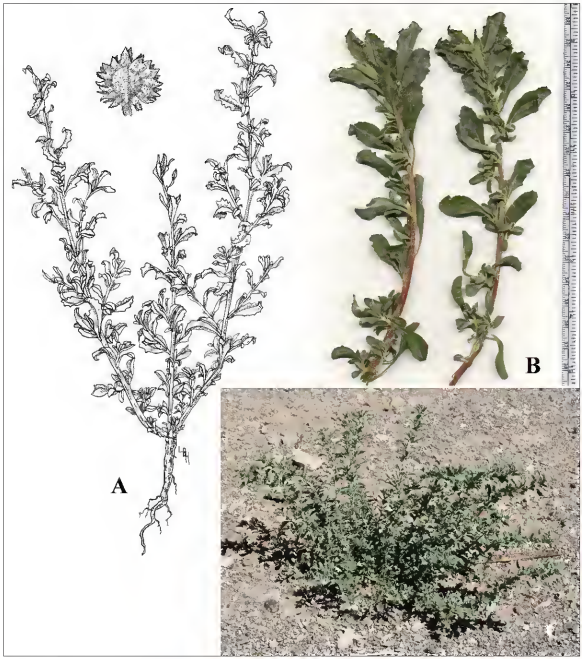

Figure 19. *Atriplex elegans*. (A) Plant and fruiting bracts; (B) international boundary near El Huerfano, 5 Mar 2014, (C) Ajo, 6 May 2006.

Atriplex lentiformis (Torrey) S. Watson subsp. **lentiformis**
Quail bush, lens scale, big saltbush; *chamizo grande*. Figure 20.

Mound-shaped shrubs often 2–2.5 m tall. Leaves 3–5 × (1.5) 2–4 cm; petioles well developed, the blades triangular, triangular-hastate, rhombic, ovate, or oblong, grayish blue, and relatively thin. This species can have male and female flowers on the same or separate plants. Fruiting bracts (2) 3–3.5 mm wide, often lens-shaped, sometimes longer than wide, flattened with shallow, blunt teeth, and not winged. Flowering and fruiting in spring and summer-fall. This species is distinguished from other Sonoran Desert saltbushes by its large size, and large, broad, and relatively thin leaf blades and well-developed petioles.

Formerly present in low-lying alkaline soils near the pond at Quitobaquito and on low hills near the spring. By 1999 there were only two plants on the eastern spring slope and none were seen in 2012. It is common along the Río Sonoyta in nearby adjacent Sonora (Felger 2000).

Deserts in western Arizona, California, Nevada, Utah, Baja California, and northwestern Sonora. Another subspecies occurs from the Mojave Desert in California to Utah.

OP. Quitobaquito. *Nichol 28 Apr 1939, Rutman 23 Apr 1999* (ORPI).

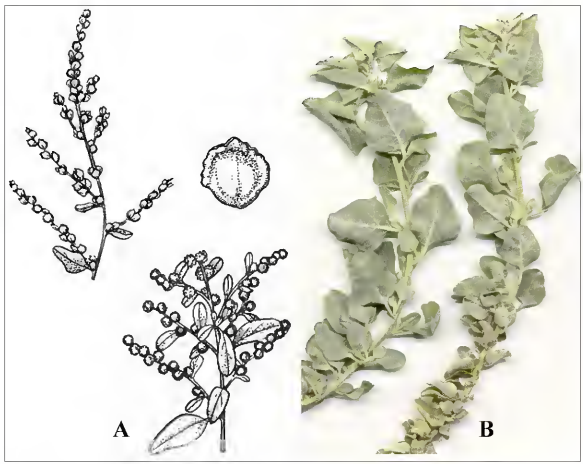

Figure 20. *Atriplex lentiformis* subsp. *lentiformis*. (A) Staminate (lower) and pistillate (upper) branches and fruiting bracts, (B) Gila River near Hwy 85, 4 Apr 2002.

Atriplex linearis S. Watson
[*A. canescens* (Pursh) Nuttall subsp. *linearis* (S. Watson) H.M. Hall & Clements]
Narrowleaf saltbush. Figure 21.

Small shrubs with upright stems. Leaves linear to narrowly oblong and keeled, the larger leaves often 1–3 (4+) cm × 2–4 mm. Male and female flowers on separate plants; reproductive mostly spring and summer. Fruiting bracts narrowly 4-winged. *A. linearis* distinguished from *A. canescens* and by overall smaller size, smaller and narrower leaves, smaller fruits, and often more pronounced (more deeply laciniate) teeth on the bracts.

Figure 21 *Atriplex linearis* (A) Pistillate branch, MEX Hwy 2, international boundary E of Quitobaquito, 5 Oct 2013; (B & C): International boundary near El Huerfano, Sonora, 6 Feb 2014: fruiting branches

Locally common on alkaline flats or semi-alkaline soils of lower bajadas, floodplains, and playa margins. Often growing with *A. polycarpa* and apparently more salt-tolerant than *A. polycarpa* and less salt-tolerant than *Suaeda nigra*.

Southeastern California, both Baja California states, southwestern Arizona, and coastal Sonora south to the Río Mayo delta and perhaps northwestern Sinaloa.

Often treated as a subspecies of *A. canescens* or sometimes regarded as distinct species (e.g., Felger 2000). They are geographically sympatric but occupy different habitats in many places in the Sonoran Desert, from at least near Phoenix, Arizona, to the Guaymas region in Sonora. Plants of intermediate character have not been seen in those places.

OP: Quitobaquito: *Nichol 10 Mar 1939* (ORPI), 24 Oct 1990, *Felger 90-488*. Dos Lomitas, *Warren 17 Nov 1974*. Cipriano Well, *Rutman 30 Aug 2001* (ORPI).
CP: Las Playas, 31 Jan 1992, *Felger* (observation).

Atriplex pacifica A. Nelson
Pacific orach. Figure 22.

Winter-spring to early summer annuals as small as 5 cm tall and upright to spreading and 40 cm across; often semi-succulent, densely short-branched, forming tangled masses. Leaves elliptic, obovate, or oblanceolate, uniformly scurfy gray on both surfaces, mostly 7–20 mm long, the margins mostly entire; lower leaves sometimes petioled. Male and female flowers on the same plant. Fruiting bracts (1) 1.2–1.5 mm wide, mealy, mostly obovoid, truncate at tip, cuneate at base, with 3 or 5 apical teeth; bracts usually with a keel or ridge and a tubercle or spine often on each side of the ridge.

Roadsides, natural desert pavements, bajadas, and arroyo or washes, and partially barren flats. In Arizona localized along the eastern and southern margins of Cabeza Prieta and in Organ Pipe near the Mexico border west of Lukeville.

Also western Sonora southward near the coast between Puerto Libertad and El Desemboque San Ignacio, and widespread and common in coastal areas of the Pacific side of the Baja California Peninsula and southern California, where the plants are often robust and 30–100 cm wide.

The distribution in Arizona and Sonora is patchy, the plants tend to be small, and the populations tend to be small and localized, which hints at colonization by individual plants. The earliest collection from Arizona or Sonora is 1966. It might be a relatively recent introduction from the Pacific coast where it is much more widespread (Felger 2000).

OP: Puerto Blanco Drive, 2-way section: ca. 10 mi W of Hwy 85, 11 Apr 1978, *Bowers 1225*; 7 mi W of Hwy 85, 10 May 1979, *Bowers 1721*.
CP: 6 mi E of Papago Well on Camino del Diablo, 13 Apr 1983, *Elber 7*. San Cristobal Wash, 20 Mar 1992, *Harlan 40*.

Atriplex polycarpa (Torrey) S. Watson
Desert saltbush, allscale saltbush; *chamizo cenizo*; 'onk 'i:vakĭ. Figures 23.

Woody shrubs, often long-lived, much branched with slender twigs, gradually becoming leafless or nearly so during extended drought. Leaves highly variable and small, the larger ones 5–20 mm long, gray-green to whitish, elliptic to spatulate; dry-season and short-shoot leaves seldom more than 10 mm long. Male and female flowers on separate plants. Flowering in various seasons, especially with hot weather following rains. Fruiting bracts usually 4–6 mm wide, somewhat orbicular to obdeltoid, often with 7–17 finger-like blunt teeth, varying in size and shape and often obscured by dense scurfy white hairs. Fruits strongly malodorous. Often with characteristic pink galls in the upper branches and inflorescences.

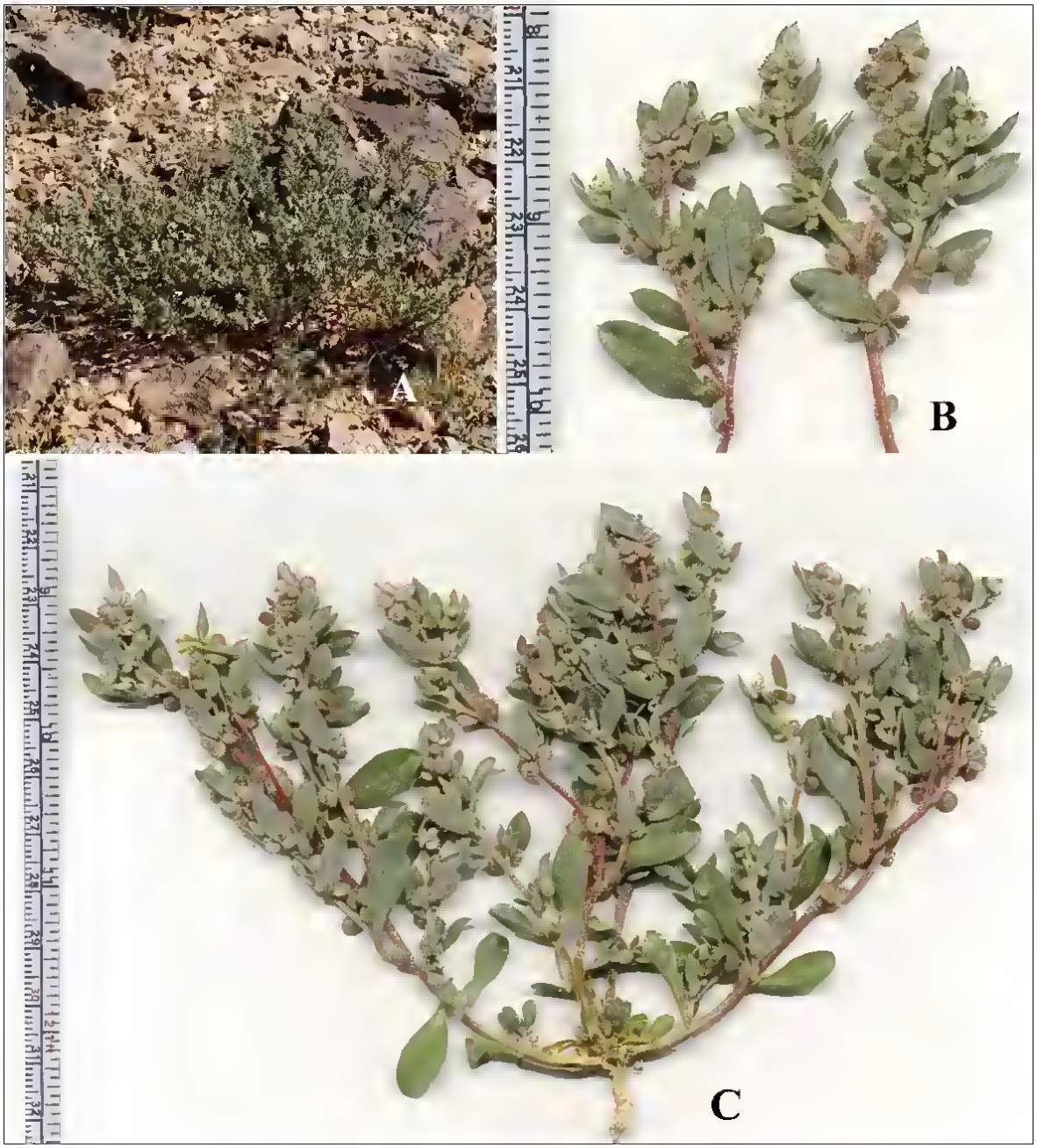

Figure 22. *Atriplex pacifica*. (A) Low hills surrounded by dunes, 20 mi S of Sonoyta on MEX Hwy 8, Sonora, 20 Feb 2014; (B & C) roadside of Mexico Hwy 2 near El Huerfano, Sonora, 5 Mar 2014.

Locally common on a surprising variety of habitats, especially alkaline or saline soils or bedrock, sandy to rocky soils of desert plains, washes, and slopes to peak elevations on the drier mountains. Often on tuff bedrock, with hop bush (*Dodonaea*) usually an associate, and creosotebush (*Larrea*) and narrowleaf saltbush (*Atriplex linearis*) absent; for example, a patch of this vegetation is at the saddle between Boulder and Arch Canyon in the Ajo Mountains.

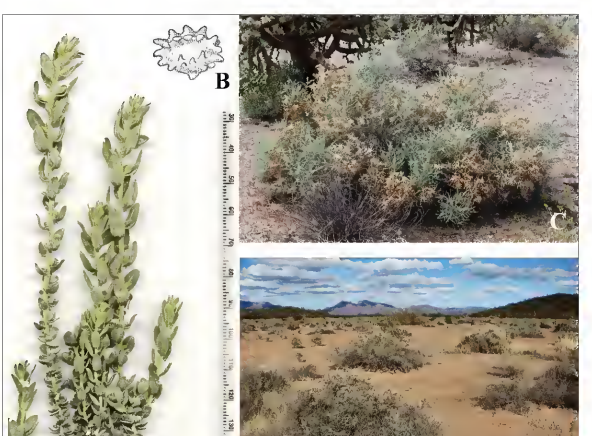

Figure 23. *Atriplex polycarpa*. (A) Near Dos Lomitas, 28 Feb 2008; (B) fruiting bracts, (C) floodplain of Rio Sonoyta near Agua Dulce west of Sonoyta, Sonora, 6 Feb 2014, (D) Dos Lomitas, 25 Jan 2008.

Packrat midden samples from the Ajo Mountains that are probably this species date from more than 29,000 years ago.

Deserts in southern and western Arizona, Nevada, southern California, the Baja California Peninsula, and western Sonora.

The seeds were eaten (Castetter & Bell 1951) and perhaps used as a famine food by the Hohokam around Phoenix (Bohrer 1985 in Hodgson 2001). An infusion of mashed young shoots was used by the Seris as shampoo and laundry detergent (Felger & Moser 1985).

OP. Quitobaquito. *Nichol 10 Mar 1939*, 23 Oct 1987, *Felger 87-268*. W of Gachado Line Camp, *Wirt 20 Mar 1989* (ORPI). Vicinity of Cipriano Well, *Rutman 30 Aug 2001* (ORPI). †Probably *A. polycarpa*. Alamo Canyon, leaves, fruits, 1150 to 29,110 ybp (3 samples); Montezuma's Head, leaves, fruits, 20,490 ybp.

CP. 1.2 miles NW of Tule Well Camp, *Van Devender 9 Mar 1980*. Charlie Bell Well, 26 Sep 1992, *Harlan 311* (CAB). Observations: Tule Tank, 2 Feb 1992, *Felger*; Buckhorn Tank, Papago Well, Tuseral Tank, 12–14 Jun 1992, *Felger*.

TA. Camino del Diablo, E of Raven Butte, 10 Jan 2002, *Felger 02-04*. SW side of Tinajas Altas Mts, flats and granitic hills, 10 Jan 2002, *Felger* (observation). †Butler Mts, leaves, 10,360 ybp.

****Atriplex wrightii** S. Watson.

Bushy annuals, often germinating in winter-spring and maturing early summer to fall. Monoecious. Fruiting bracts more or less obdeltoid, with 5 or 7 terminal teeth.

Not known from the flora area but documented just south of the Organ Pipe in the vicinity of Sonoyta and probably not native to that region, as it occurs only in disturbed habitats. Western Texas to central and southern Arizona and northern Sonora.

Sonora: Sonoyta, 4 Oct 1985, *Felger 85-928*.

Figure 24. *Bassia hyssopifolia*. (A) Plant, fruiting calyx, seeds, and portion of spike, (B) construction area, Hwy 85 at Cherioni Wash crossing, 13 Apr 2005.

****Bassia hyssopifolia** (Pallas) Kuntze
Smother weed. Figure 24.

Leafy annuals with a well-developed main stem, usually germinating in spring and maturing in fall. The hooked spine at the end of each of the 5 calyx lobes is unique among the plants of this flora.

The two specimen records for Organ Pipe grew from seeds in straw imported from California and used to control erosion at construction sites. It is abundant primarily as an agricultural weed around Sonoyta adjacent to the southern margin of the monument and can be expected to spread into the monument on the heels of disturbance.

Native to Eurasia; widespread weed in western North America since its reported introduction in Nevada around 1915.

OP Hwy 85, roadside at Cherioni Wash, ca 4.7 mi N of Park headquarters, *Rutman 15 Apr 2005* (ORPI)

Figure 25 *Chenopodiastrum murale*. (A) Flowering plant with fruiting calyx and seed; (B) international boundary near El Huerfano, Sonora, 5 Mar 2014

***Chenopodiastrum murale** (Linnaeus) S. Fuentes, Uotila & Borsch
[*Chenopodium murale* Linnaeus]
Netleaf goosefoot; *chual, choal*; 'onk 'i:vakĭ, kaupdam. Figure 25.

Winter-spring annuals, sometime persisting into summer in well-watered, shaded habitats. Herbage green or often reddish green, sometimes semi-succulent. Leaves alternate, glabrous or sometimes gray scurfy below, often 3–10 cm long, the blades mostly ovate to rhombic, irregularly toothed, the petioles well developed. Flowers bisexual. Sepals often keeled, mostly partially spreading at maturity to reveal part of the seed. Seeds 1.2–1.4 mm wide, lens-shaped, blackish, mostly devoid of dried pericarp, dull even after removal of pericarp, the margins acute with a thin rim.

Widespread; washes, canyon bottoms, damp soil at tinajas and waterholes, dirt tanks, and especially at improved waterholes and disturbed habitats.

Reported as not native in the New World, although long established and widespread in the Sonoran Desert with a long history of use in the region. Young plants were eaten as greens (Castetter & Bell 1951; Castetter & Underhill 1935). The seeds were toasted and ground into flour, and are apparently the only edible seeds in the region that open like popcorn when heated (Felger 2007; Felger & Moser 1985).

Fuentes et al. (2012) separated five former species of *Chenopodium* as *Chenopodiastrum* to form a monophyletic genus occurring in Africa, Eurasia, and North America.

OP: Quitobaquito, *Nichol 28 Apr 1939*, 13 Sep 1988, *Felger 86-269*. Gachado Line Camp, 27 Jan 1978, *Bowers 1015*.
CP: Tule Tank, 2 Feb 1992, *Felger 92-65*. Jose Juan Tank, 26 Feb 1993, *Felger 93-106*. Charlie Bell Well, 10 Apr 1993, *Felger 93-366*.
TA: Tinajas Altas, 19 Mar 1998, *Felger 98-149*.

Chenopodium cf. **watsonii** A. Nelson
Watson's goosefoot. Figure 26.

Winter-spring annuals. Leaves alternate and petioled. Herbage often pale grayish green, and mealy with inflated whitish hairs. The entire plant is very stinky, even when young—some say it smells like rotten fish. Flowers bisexual. Seeds lens-shaped, ca. 1 mm wide, the surfaces covered by a translucent pericarp forming a minute cellular pattern (like minute honeycomb depressions), the seeds shiny blackish after removal of this covering, the margins obtuse (without a distinct rim).

Apparently all the stinky chenopodiums in the region are this species, characterized by odor, leaf shape (variable but often more or less rhomboid) and color (pale and mealy on both surfaces), and mature calyx covering the seed. The pericarp (the thin seed covering) is distinctly white-waxy; sometimes, however, even mature fruits may lack the distinctive full white pericarp although there will be some whitish cells, so the pericarp, while waxy, is mostly black and only partly whitish.

Widely scattered, in small to large populations but seldom abundant; generally on rocky slopes and canyons in the Ajo and Puerto Blanco Mountains.

Alberta and Saskatchewan to southern Arizona and New Mexico, and undoubtedly adjacent northern Sonora and Chihuahua.

The name goosefoot derives from the leaf shape of certain species. *Chenopodium*, with about 150 species, is worldwide.

OP: Dripping Springs, 29 Jan 1978, *Bowers 1019* (ORPI). Alamo Canyon, *Van Devender* 31 Aug 1978 (ORPI). Trail from The Cones to Mount Ajo, 4090 ft, 10 Apr 2005, *Felger* (observation).
Puerto Blanco Mts, Dripping Wells, 2600 ft, rocky NE slope, herbage with fetid odor, 18 Mar 1945, *Gould 3016* (as *C. fremontii* S. Watson, det. H.A. Wahl 1966).

Figure 26. *Chenopodium* cf. *watsonii*. Alamo Wash: (A) 30 Jul 2013; (C) 11 Mar 2014. (B) S of Animas in Hidalgo Co., New Mexico, 19 Aug 2010, photo by Patrick Alexander (SEINet).

†††**Froelichia** sp.

There is a fossil specimen 13,500 years old from the Ajo Mountains. It is likely to be *F. arizonica* Thornber ex Standley, an herbaceous perennial, often short-lived and mostly growing and flowering with summer rains. The flowers are inconspicuous and nearly hidden in woolly bracts.

The nearest present-day population is in the Baboquivari Mountains. It ranges from southern Arizona to west Texas and Sonora to Coahuila and Nuevo León.

The fossil is less likely to be *F. gracilis* (Hooker) Moquin-Tandon, an annual with the nearest populations in central and southeastern Arizona, and ranges from eastern and central United States to northern Mexico.

OP: Montezuma's Head, achene, 13,500 ybp.

Gomphrena sonorae Torrey

Sonoran globe amaranth. Figure 27.

Annuals or short-lived herbaceous perennials; mostly responding to summer-fall rains, and sometimes weakly re-growing with winter-spring rains; usually few-branched and taller than wide. Leaves mostly basal, green, elliptic to oblanceolate or linear, often 3–10 cm long, sessile or short-

Figure 27. *Gomphrena sonorae*. (A & C) Garden Canyon, Huachuca Mts, photo by Liz Makings (SEINet), (B) Patagonia Mts area, Cochise Co., 17 Aug 2011, photo by Eugene Sturla (SEINet).

petioled. Flowers 3.5–4 mm long, crowded in rounded clusters among papery white bracts and nearly hidden among cottony white hairs. Sepals separate, rather papery and not firm, the tips acute.

In the flora area known only from Bull Pasture in the Ajo Mountains. Sue Rutman has tried, to no avail, to find this plant again in the Ajo Mountains.

Arizona and southwestern New Mexico to western Mexico including the Baja California Peninsula.

OP: Bull Pasture. 3300 ft, *Henry probably 1977 or 1978* (ORPI), Wash, *Wirt 13 Nov 1989* (ORPI).

Monolepis nuttalliana (Schultes) Greene
Poverty weed; ʼopoñ. Figure 28.

Low-growing winter-spring annuals; plants semi-succulent, spreading to semi-prostrate with age and size, the stems often 5–25 cm long. Larger leaves mostly 1–5 cm long, the petioles expanding into lanceolate to linear blades with hastate "ears," the smaller leaves often entire, leaves reduced upwards to leafy bracts. Flowers unisexual or bisexual, in dense, sessile, axillary clusters; flowers minute and inconspicuous, floral parts greatly reduced, the calyx usually of 1 persistent green sepal, the stamens 1 (2) or none. Seeds 0.9–1.2 mm wide, flattened, lens-shaped, dull beneath a thin, persistent pericarp with a honeycomb-alveolate pattern.

Sandy gravelly and silt-clayish soils of washes, canyon bottoms, and dirt tanks. Widely scattered in the northern and eastern part of Organ Pipe and known by one record from Cabeza Prieta.

Alaska and Canada to northern Mexico and in Argentina; adventive in the Old World. Desert populations in western North America have much narrower and smaller leaves than those from more humid, temperate regions. *Monolepis* might be confused with *Cistanthe monandra* (Portulacaceae), which has entire leaves and multiple-seeded fruits.

This spring annual was widely used as greens. Betty Melvin mentions a "wild spinach . . . they eat . . . [called] *opon*" (Zepeda 1985: 73). The seeds are also edible (Hodgson 2001).

OP: Tres Alamo Canyon, 2700 ft, *Nichol 24 Feb 1939*. Sandy flats near old ranch by Kuakatch Wash at N boundary [Armenta], 30 Mar 1978, *Bowers 1160*. Mouth of Alamo Canyon, *Rutman 15 Mar 2003* (ORPI).
CP: Redtail Tank in silty-clayish soil next to the represo, locally abundant, 25 Feb 1993, *Felger 93-77*.

Figure 28. *Monolepis nuttalliana*. Vicinity of Lost City, San Cristobal Valley, Cabeza Prieta, 13 Mar 2014.

Nitrophila occidentalis (Moquin-Tandon) S. Watson
Alkali weed. Figure 29.

Highly succulent herbaceous perennials from deep, thick succulent rhizomes to 2.5 cm in diameter and 15+ cm deep; above-ground parts are freeze-killed with frost, new shoots rapidly appear in early spring. Stems much-branched. Leaves sessile, succulent and linear, mostly 1–2.5 cm long, the lower leaves clasping the stems. Flowers bisexual, 1 or 3 in leaf axils, subtended by 2 leaf-like bracts of unequal size. Calyx lobes and stamens 5, the calyx 2.5–4 mm long, fleshy, green outside, pink within, persistent when dry with a midrib keel. Seeds 1.4–1.5 × 1.2 mm, D-shaped, smooth and shining, dark red-brown to blackish. Flowering at least March and April.

Figure 29. *Nitrophila occidentalis*. Quitobaquito: (A) 19 Mar 2008, (B & C) 5 May 2005.

Locally common in alkaline/saline wet soils at Quitobaquito. Deer paw the ground to expose and eat the rhizomes and shoots.

Saline/alkaline wetlands in southwestern Arizona, northwestern Sonora, and northeastern Baja California to Oregon and Nevada.

OP: Quitobaquito: *Nichol 28 Apr 1939*, between Quitobaquito and Burro Spring, with *Suaeda torreyana, Haplopappus acradenius*, 14 Jun 1978, *Bowers 1333*; Hypersaline soils wetted by Quitobaquito Springs, to the NE of Quitobaquito Pond, with *Juncus mexicanus, Eleocharis rostellata*, 15 June 2013, *Rutman 20130615-2*.

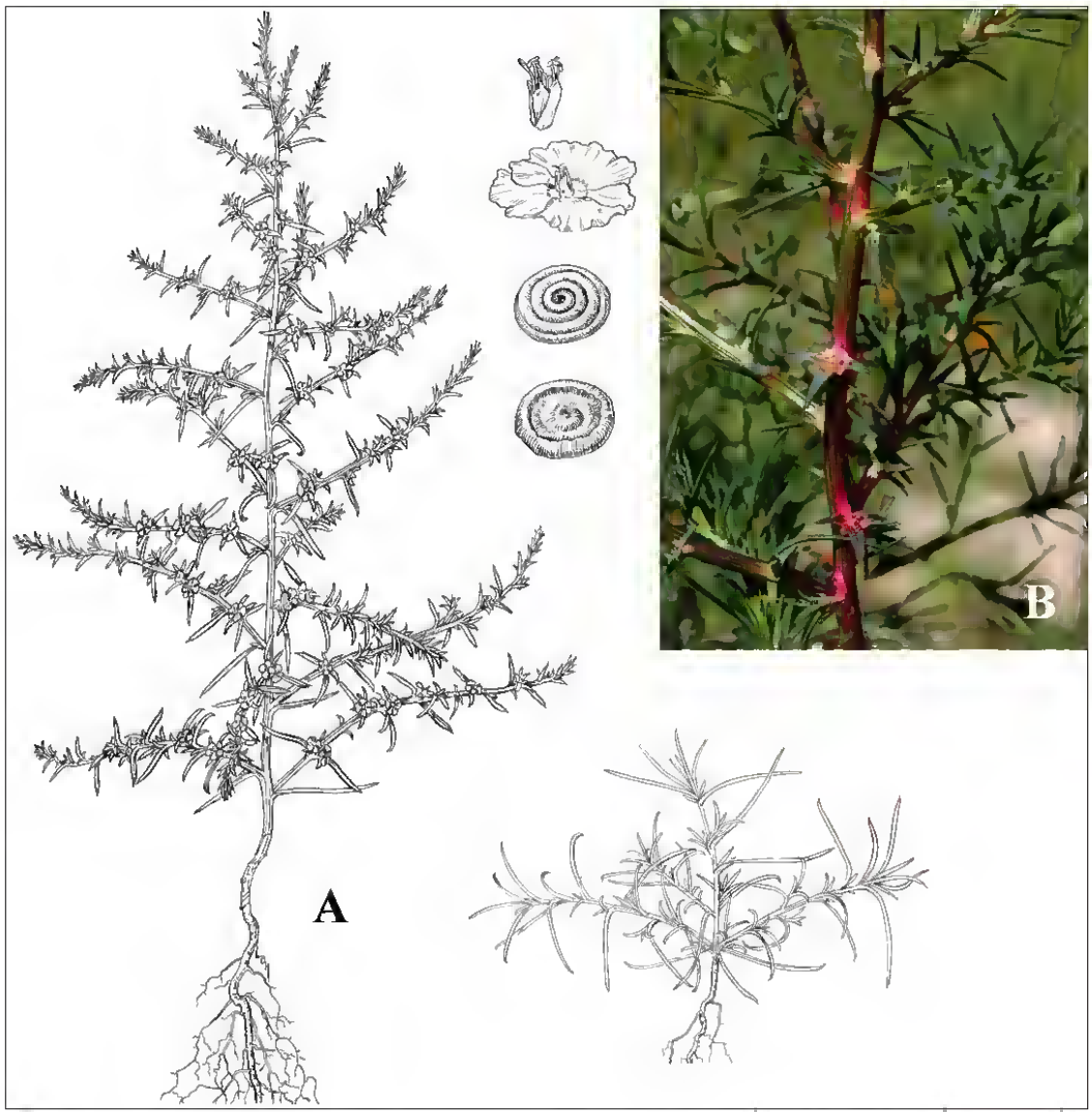

Figure 30. *Salsola tragus*. (A) Plant, male flower (above), female flower with sepals, seed, fruit, and seedling, (B) Ajo, 26 Feb 2005.

***Salsola tragus** Linnaeus
[*S. australis* R. Brown. *S. iberica* (Sennen & Pau) Botschantzev ex Czerepanov. *S. kali* of authors, not *S. kali* Linnaeus. *S. kali* var. *tenuifolia* Tausch ex Moquin-Tandon. *S. pestifer* Nelson]
Russian thistle, tumbleweed; *chamizo volador*; hejel 'e'esadam, vo'po'odam sa'i. Figure 30.

Warm weather annuals, germinating in spring or with the summer rains, plants globose at maturity at the end of summer or fall, breaking off at ground level to become tumbleweeds. Lower or seedling leaves often linear to thread-like, semi-succulent; upper leaves 1–2.5 cm long and spinescent-tipped. Flowers bisexual, in upper leaf axils, subtended by ovate, spinescent bracts 5–8 mm. Fruiting calyx pink to white, with collar-like wings often 5–6.5 mm wide. Seeds fall with the calyx.

Disturbed habitats, mostly roadsides and along washes. Populations decline over time as sites recover from disturbance. A fire east of Dos Lomitas in 2000 (Martin Fire) was carried by tumbleweeds that had piled up against the boundary fence and spilled into Organ Pipe. People on the Mexican side of the border were burning "weeds" in farm ditches and the fire got out of control.

This C4 plant is native to Eurasia and has become a troublesome weed worldwide, especially on disturbed soils in hot, dry regions.

OP: Puerto Blanco Drive, 10 mi W of Hwy 85, 10 May 1979, *Bowers 1720*.
CP: Childs Mt. *Simmons 30 Oct 1963* (CAB). 2300 ft, 18 Aug 1992, *Felger 92-644*.

Figure 31. *Suaeda nigra*. Quitobaquito (A & B) 11 Sep 2008, (C) 22 Jun 2006

Suaeda nigra (Rafinesque) J.F. Macbride
[*S. moquinii* (Torrey) Greene. *S. torreyana* S. Watson]
Seepweed; *quelite salado*; s-cuk onk. Figure 31.

Densely-branched, mound-shaped succulent shrubs often 1–2 m tall, branched throughout with many spreading, interlacing branches; foul smelling when crushed. Stems slender and brittle. Herbage green to glaucous blue-green and often reddish purple. Leaves alternate and succulent, the long-shoot leaves linear, often 10–30 mm long, the short-shoot leaves usually crowded, 3–8 mm long and bead-like. Flowers minute, mostly produced during the warmer months. Flowering branches slender and paniculate. Flowers 1–ca. 10 per cluster, often functionally unisexual. Sepals 5, succulent and hooded, unequal in size in female flowers, the fruiting calyx bilateral, often 1.3–1.6 mm wide. Seeds 1–1.5 mm diameter.

Locally common on saline or alkaline soils. Washes and near springs and waterholes in the southwestern margin of Organ Pipe from the vicinity of Ten Mile Hill to the southwestern corner (see *Wislizenia refracta*) and the vicinity of Dos Lomitas. Cabeza Prieta along the large xeroriparian washes at Tule Well and on temporarily wet soil near Papago Well.

Alberta and the western United States to northern and central Mexico.

Seepweed was cooked by Gila River Pimas as greens, used for flavoring in cooking other foods, or added to cactus fruit for flavor. It was also used to line a pit for baking cholla buds of *Cylindropuntia acanthocarpa* (Curtin 1949; Rea 1997; Russell 1908). Young tender plants of this or a similar species, called *romerillo*, are a well-known vegetable in southern Mexican cuisine.

OP: Quitobaquito, *Nichol 3 Mar 1939*. Williams Spring, *Van Devender 30 Aug 1978*. 3.5 mi E of Aguajita, 24 Oct 1990, *Felger 90-472B* (ORPI). Dos Lomitas, *Rutman 24 Jul 2002* (ORPI). Hocker Well, 3 Dec 1990, *Felger* (observation).
CP: Tule Well, 27 Nov 2001, *Felger 01-544*. Papago Well, 13 Jun 1992, *Felger* (observation).

Tidestromia lanuginosa (Nuttall) Standley subsp. **eliassoniana** Sánchez-del Pino & Flores Olvera [*T. eliassoniana* Sánchez-del Pino]
Woolly honeysweet; *hierba ceniza, hierba lanuda*. Figure 32.

Summer-fall ephemerals, sometimes persisting until December but perishing with the first near-freezing temperatures. Plants often low and spreading, or the larger plants mound-shaped; stems often reddish. Pubescence dense and scurfy-whitish, with small, branched hairs (candelabriform; unique for the family in the flora area), often obscuring the leaf surfaces, or the plants sometimes more sparsely pubescent when well-watered. Leaves mostly opposite, occasionally alternate, petioled, the blades broadly obovate to orbicular, reduced and congested upwards and appearing whorled, the lower leaves often 1.5–3.5 (4.5) cm long, soon withering. Flowers bisexual, 2–2.5 mm wide and yellow, each produced in a small cup-shaped involucre growing around the flower; new involucres produced from the margin of the cups of older involucres; this proliferation results in highly clustered inflorescences, which continue through the season as long as moisture and warm weather hold out. Seeds globose.

Seasonally common and widespread across the flora area, especially at lower elevations on silty, sandy, and gravelly soils of desert flats, bajadas, washes, and roadsides, as well as rocky slopes and dunes. The above-average rainfall in the Organ Pipe region in 2012 was a banner year for *Tidestromia*. The plants were so large they overtopped *Ambrosia deltoidea* and *A. dumosa* and the plants were so dense that white bands or patches of *Tidestromia* could be seen on lower mountain slopes.

Two subspecies can be distinguished by presence or absence of decorations on the ends of the terminal arms of the branched hairs and pollen differences. Although the distinctions seem minor, they are geographically segregated. Subspecies *eliassoniana* occurs west of the continental divide in southwestern North America and subsp. *lanuginosa* occurs east of the divide (Sánchez-del Pino & Clemants 2003).

OP. Armenta Well, *Warren 16 Nov 1974*. Bull Pasture trail, 5 Nov 1977, *Bowers 952* (ORPI). Aguajita, wash, 14 Sep 1988, *Felger 88-408*

CP. Daniels Arroyo at Charlie Bell Rd, 18 Aug 1992, *Felger 92-666*. Pinta Sands, 15 Sep 1992, *Felger 92-761*

TA. Coyote Water, 25 Oct 2004, *Felger 04-64*. Tinajas Altas, 19 Mar 1998, *Felger* (observation, dry plants from previous year).

Figure 32. *Tidestromia lanuginosa* subsp. *eliassoniana*. Growler Valley, Organ Pipe. (A) 9 Sep 2008, (B) 8 Oct 2006. W of mile 60, Hwy 85. (C) 6 Oct 2012, (D) 30 Sep 2006.

ANACARDIACEAE – Cashew Family

Rhus – Sumac

Shrubs; leaves alternate, stipules none. Flowers bisexual or unisexual, small, 5-merous, with a ring-shaped nectary disk between the stamens and ovary. Fruit a small drupe.

1. Leaves simple (or sometimes also a few leaves with 3 leaflets), tough and rather shiny, essentially evergreen. ..... **Rhus kearneyi**
1. Leaves with 3 leaflets, thin and dull, winter deciduous. ..... **Rhus aromatica**

Rhus aromatica Aiton var. **trilobata** (Nuttall) A. Gray ex S. Watson
[*R. trilobata* Nuttall]
Skunk bush; lemonade bush; *limita*. Figure 33.

Slender-stem shrubs, 1.8–2.3 m tall. Leaves winter deciduous, (1.4) 2–4 cm long; leaflets 3 and thin, the margins shallowly lobed. Inflorescences terminal and axillary, with spike-like branches developing with the foliage in fall, overwintering, and producing small, white flowers late February and March before the leaves appear.

The leaves are moderately stinky when crushed, hence the common name. The fruits have a lemon-like taste, thus the Sonoran name *limita* (little lime).

Canyons and slopes in the Ajo Mountains, especially at higher elevations and on north-facing slopes. Another isolated, relictual population occurs at higher elevations in the Sierra Pinacate in nearby Sonora (Felger 2000).

It has been in the Ajo Mountains for at least 29,000 years ago. The fossil record indicates it was far more common in the late Wisconsin and early Holocene than today. It no longer grows near the rock shelters (Alamo Canyon and Montezuma's Head) where the middens were found. A similar or the same species grew at Tinajas Altas from at least about 9250 to 11,000 years ago.

This species complex ranges from Canada to southern Mexico and is taxonomically confusing with variously recognized varieties.

OP: Alamo Canyon, 18 Dec 1939, *Harbison 25670*. Arch Canyon, 1 Apr 1976, *Scaggs 2131*. Bull Pasture, *Wirt 12 Nov 1989*. (ORPI). †Alamo Canyon, seeds, 8130 to 29,110 ybp (6 samples, probably this species). †Montezuma's Head, seeds, 13,500 & 20,490 ybp
TA: †*R.* cf *trilobata*, Tinajas Altas, seeds, 9230 to 11,040 ybp (5 samples)

Rhus kearneyi F.A. Barkley subsp. **kearneyi**
Desert sumac; *limita del desierto*. Figure 34.

Hardwood shrubs often 1.5–3.5 m tall, densely branched with dense foliage and relatively tough, inflexible branches. Leaves simple (rarely 3-lobed on long-shoots), 3.5–8.5 × 2–3.8 cm, ovate and entire, tough, bicolored, shiny green to somewhat bluish glaucous; leaf margins entire or sometimes irregularly undulate or serrate even on the same plant; crushed leaves have a fruity odor. Characteristically evergreen, but the leaves gradually shed during extended drought; the ground beneath the shrubs littered with dry leaves. During severe freezing weather in January 1987, cultivated plants in Tucson defoliated but rapidly recovered.

Inflorescences terminal, spike-like or paniculate, compact and densely flowered, mostly 1.5–3 cm long. Flowers white or pink; about 5 mm long; nectary disk of young flowers glistening yellow, with age becoming maroon-red. Fruits ripe November–March, ca. 1 cm long, orange and slightly fleshy when ripe, the surface covered with glands and wet with gooey but not sticky exudate, this liquid has a pleasant, tart (acidic) or citrus-like favor.

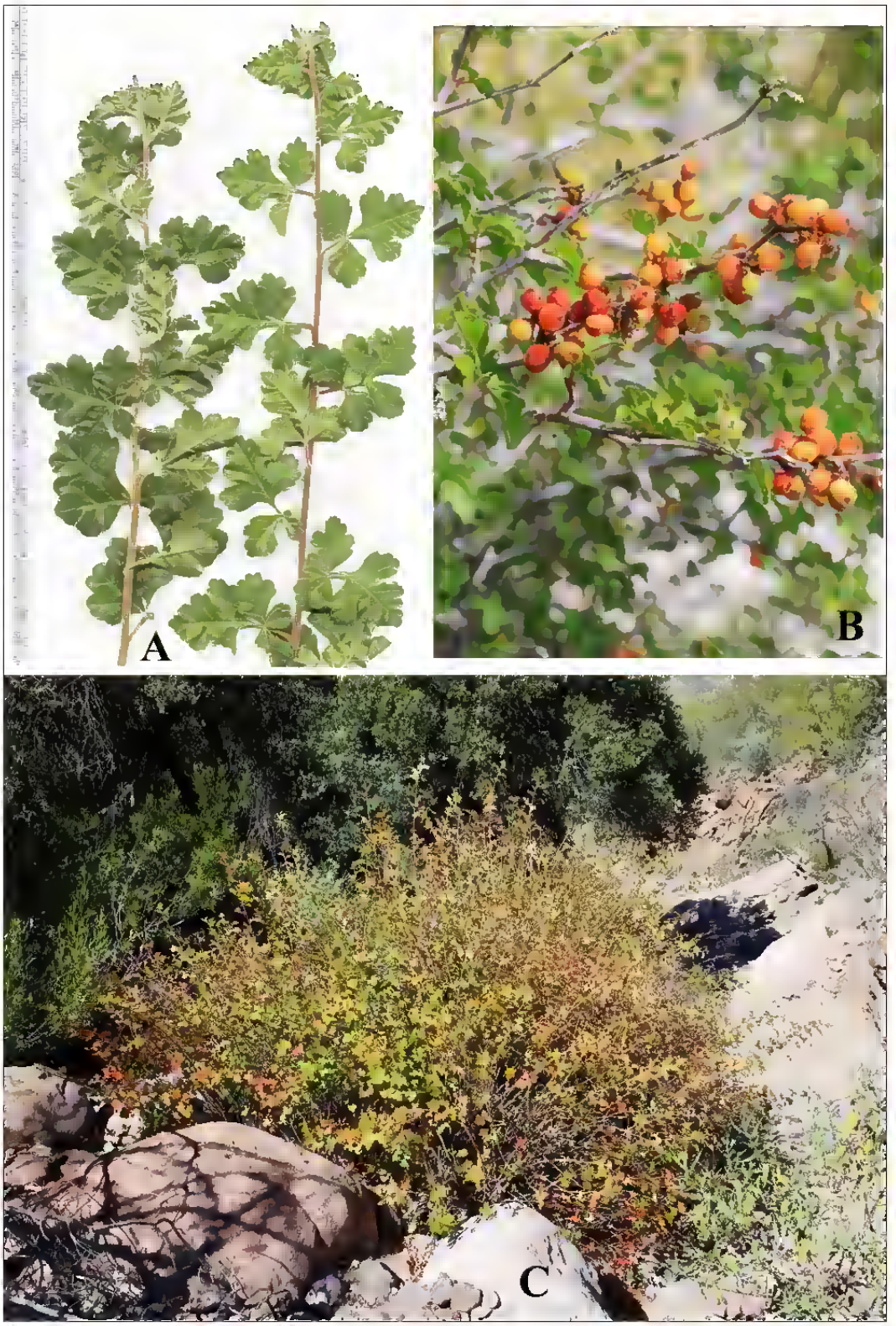

Figure 33. *Rhus aromatica* var. *trilobata*. Alamo Canyon, above Alamo Well: (A) 17 Oct 2013, (C) 12 Jan 2013. (B) Palm Canyon, Joshua Tree National Park, CA, 1 May 2012.

Figure 34. *Rhus kearneyi* subsp. *kearneyi*. Steep, N-facing granite slope S of MEX Hwy 2, Sierra Nina (= Sierra del Águila), Sonora, 17 Mar 2014.

Concentrated in steep canyons and cliff bases on precipitous north-facing mountain slopes of the Cabeza Prieta, Tinajas Altas, and Gila Mountains, and adjacent granitic mountains in Sonora.

Disjunct populations of this subspecies also occur in Sonora in the Sierra del Viejo southwest of Caborca and in Baja California in the Sierra San Pedro Mártir. Two other subspecies occur in mountains of Baja California and Baja California Sur. *Rhus kearneyi* seems most closely related to *R. integrifolia* of the Pacific coast of the Californias.

CP: Cabeza Prieta Mts: Silver Star Canyon, *Simmons 27 Sep 1964*; Cabeza Peak, 14 Feb 1973, *Niehaus 980*.

TA: Tinajas Altas, 20 Nov 1913, *Goldman 2311* (US). Tinajas Altas Mts, 29 Mar 1930, *Harrison & Kearney 6573* (isotype). Borrego Canyon, 16 Jun 1992, *Felger 92-612*.

APIACEAE (UMBELLIFERAE) – Carrot or Parsley Family

Five species in the flora area are winter-spring annuals and one is an herbaceous perennial. Leaves alternate, sometimes in basal rosettes. Flowers small and radial. Perianth 5-merous; calyx reduced or absent; petals separate or absent; stamens 5; styles 2. Fruits dry, with 2 one-seeded segments (mericarps) almost always separating at maturity.

The *Daucus*, *Spermolepis*, and *Yabea* species are somewhat similar in appearance, but are readily distinguished by features given in the key.

1. Low-growing perennials with a thickened rootstock; Ajo Mountains. ..... **Lomatium**
1. Cool-season annuals with slender roots or a single tap root; various localities.

2. Plants stemless or with weak and trailing stems; herbage and fruits with stellate hairs; leaves simple, the blades wider than long, orbicular to palmately lobed. ..... **Bowlesia**
2. Plants stemless or with erect to spreading stems; glabrous or pubescent but the hairs not stellate; leaves pinnately deeply lobed or toothed to divided, longer than wide.

3. Leaves coarsely toothed; bracts stiff and spinescent at maturity; flowers and fruits sessile in dense head-like or cone-shaped inflorescences. ..... **Eryngium**
3. Leaves finely divided; leaves and bracts soft, not spinescent (fruits with spines); flowers and fruits pedicelled in rather open umbels.

4. Plants glabrous or slightly roughened; fruits rounded, 1.5–2 mm in diameter. ...**Spermolepis**
4. Plants pubescent with hispid hairs; fruits ellipsoid, 2.5–6.5 mm long.

5. Spines on fruits straight and with tiny barbs at the tip (use magnification); body of fruit 2.5–3 mm long. ..... **Daucus**
5. Spines on fruits hooked but not barbed; body of fruit more than 5 mm long. ..... **Yabea**

Bowlesia incana Ruiz & Pavón
Hoary bowlesia. Figure 35.

Delicate annuals with stellate hairs. Stems 4–45 cm long, slender, weak and often trailing. Leaves simple, petioled, the blades wider than long, 10–24 mm wide, with (3) 5 or 7 broad lobes. Flowers 2–6 on unbranched stalks shorter than the petioles; flowers minute, inconspicuous, and green and sessile, the sepals and petals scale-like, 0.5 mm long. Fruits of 2 ovoid-globose segments, each 2–2.4 mm wide.

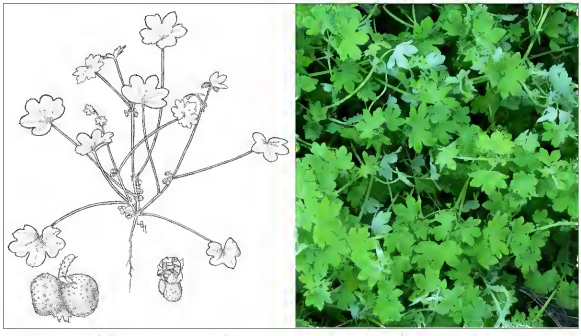

Figure 35. *Bowlesia incana*. (A) Plant, fruit (left), and flower; (B) volunteer in Ajo garden, 13 Feb 2005.

Widespread in Organ Pipe and the eastern part of Cabeza Prieta including mountains and lowland habitats, often in shaded microsites beneath shrubs, in washes, sandy flats, and on north-facing rocky slopes.

Presumed native in southwestern United States and northern Mexico, and disjunct in South America. It has spread as a weed as far as Oregon and Florida and into eastern United States. The genus is diverse in South America; *B. incana*, the only member in North America, presumably migrated from South America by natural means.

OP: Ajo Mts, 1 Apr 1944, *Clark 11550* (ORPI). 2 mi WSW of Bates Well, 30 Mar 1978, *Bowers 1132*. International fence at El Papalote, adjacent to Aguajita Spring, 9 Apr 1986, *Felger 86-101*. Alamo Canyon, *Wirt 13 Mar 1991* (ORPI).

CP: Road to Agua Dulce Pass, 19 Mar 1987, *Eltas 10202*. San Cristobal Wash, 11 Apr 1992, *Harlan & Steinmann 150* (CAB). Charlie Bell Road near E boundary of Refuge, 25 Feb 1993, *Felger 93-50*. Papago Well, 25 Feb 1993, *Felger 93-140*.

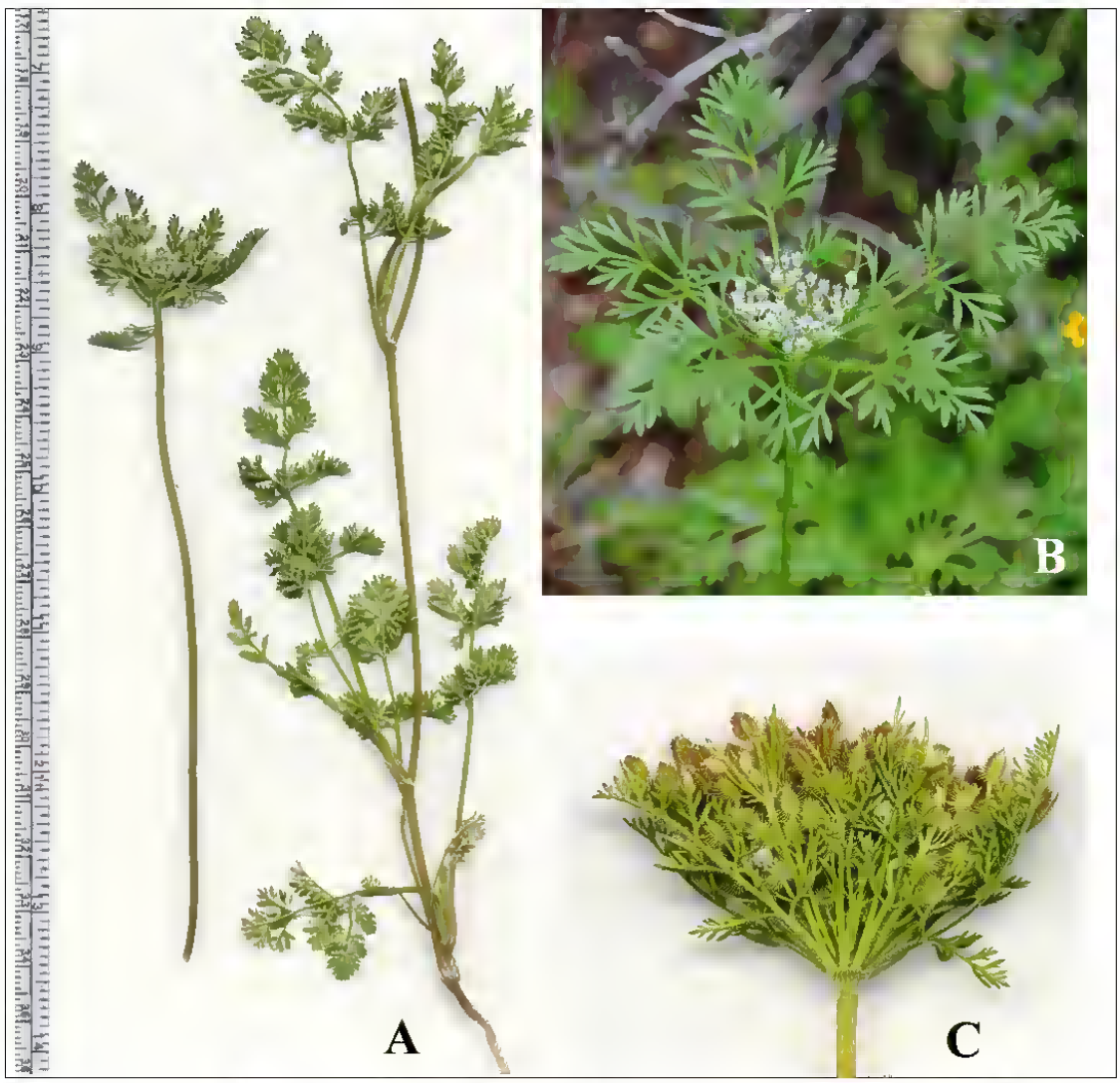

Figure 36. *Daucus pusillus*. (A) Bull Pasture, 7 Mar 2014; (B) Estes Canyon, 18 Mar 2005; (C) trail to Bull Pasture, 21 Dec 2008.

Daucus pusillus Michaux
American wild carrot; *zanahoria silvestre*. Figure 36.

Delicate annuals with stiff white (hispid) hairs sometimes bulbous-based on stems and inflorescence branches, and with a slender, orange tap root. Stems slender, 7–50 cm tall. Leaves lacey, highly dissected into small, narrow segments. Inflorescences 3.5–27 cm tall, of compound and densely flowered umbels on stout peduncles with leafy bracts. Petals 0.6 mm long, white or pale yellow. Fruits bur-like, 2.5–3 mm long, intricately sculptured with yellow barb-tipped spines.

Widespread and often common in Organ Pipe and Cabeza Prieta including washes, canyons, rocky slopes to peak elevations, and sometimes on dunes. It is one of the few winter ephemerals that grow on *Selaginella* slopes. There are no modern records from Tinajas Altas region but it grew there at least 9000 to 9800 years ago.

Western and southern United States, northern Mexico, and South America.

OP: Alamo Canyon, *Nichol 26 Mar 1939*. Senita Basin, 23 Mar 1969, *Lehto 15406-b* (ASU). Slopes NW of Pinkley Peak, *Rutman 24 Mar 2001* (ORPI). Armenta Road, 1.4 mi W Hwy 85, 11 Mar 2003, *Felger 03-266*. Middle fork of Alamo Canyon near crestline of Ajo Mts, 15 Mar 2003, *Rutman 2003-322* (ORPI).
CP: Charlie Bell Pass, 3 Apr 1992, *Whipple 3922* (CAB). Bassarisc Tank, 26 Feb 1993, *Felger 93-122*. Childs Mt, 2240 ft, 9 Apr 1993, *Felger 93-275*. Charlie Bell Road at Daniels Arroyo, 10 Apr 1993, *Felger 93-343*. Pinta Sands, 11 Apr 1993, *Felger 93-422*. Las Playas, 2 Mar 1998, *Harlan 502*.
TA: †Tinajas Altas, fruits, 8970 & 9790 ybp

Eryngium nasturtiifolium de Jussieu ex F. Delaroche
Hierba del sapo. Figure 37.

Winter-spring annuals (often biennial or perennial outside the desert), glabrous, 3–12 cm wide, usually with a stout taproot. First leaves in a basal rosette, 1.5–6+ cm long, thin, green, soon withering. Leaves pinnatifid-toothed, the teeth sharp- or spine-tipped. Inflorescences densely flowered and cone-shaped, subtended by leaf-like bracts. Flowers minute; sepals 1.6–2.5 mm long and sharp pointed; petals 0.5 mm long, white, and soon deciduous.

Figure 37. *Eryngium nasturtiifolium*. Represo de Ortega (S of Las Playas, Cabeza Prieta NWR), Sonora, 11 Apr 2014

Locally common in poorly-drained clay soils of dirt tanks and playas, growing as the water recedes. Seasonally abundant across Las Playas and Dos Playas during favorable years. In Arizona known only from Cabeza Prieta, Cameron Tank just east of Cabeza Prieta and southwest of Ajo, and near the Mexico border in the Tohono O'odham lands. It is locally common in similar habitats northwestern Sonora.

Southern Arizona, Texas, through much of Mexico, and Cuba

CP. Las Playas, 10 Apr 1978, *Lehto L22460* (*n* = 16, ARIZ, ASU). Dos Playas, 7 Apr 1979, *Lehto L-23594*. Jose Juan Tank, 26 Feb 1993, *Felger 93-96*.

Lomatium nevadense (S. Watson) J.M. Coulter & Rose
Biscuit-root. Figure 38.

Herbaceous perennials. Herbage grayish green. Leaves basal, to ca. 15 cm long, 2- or 3-times pinnately dissected. Flowers in compound umbels, dull purplish whitish and minute. Fruits ca 1 cm long, compressed, winged and ribbed.

Figure 38. *Lomatium nevadensis*. (A) Hoodoo Canyon, Burro Mts, Grant Co., NM, 23 Feb 2010; (B) Knight Mt, Burro Mts, NM, 21 Mar 2009, photos by Russell Kleinman (gilaflora.com). (C) Crest of Ajo Mts, middle fork of Alamo Canyon, 27 Mar 2005.

Locally common at higher elevations in the Ajo Mountains. The nearest population is in the Baboquivari Mountains.

Western North America and northwestern Mexico. The Ajo Mountain plants are var. *pseudorientale* (M E. Jones) Heller, although the varieties seem poorly defined

OP: Near crestline of Ajo Mts, middle fork Alamo Canyon, intershrub spaces, associated species *Juniperus*, *Nolina*, *Vauquelinia*, *Viguiera*, *Menodora*, *Simmondsia*, *Yucca*, *Selaginella*, 3400 ft, 15 Mar 2003, *Rutman 2003-333* (ORPI).

Spermolepis lateriflora G.L. Nesom
Bristly scale-seed. Figure 39.

Small annuals, glabrous. Leaves dissected into thread-like or linear segments. Flowers minute, petals white. Fruits rounded, 1.5–2 mm wide, ribbed, and with short bristles.

Along washes in the eastern part of Cabeza Prieta and widely scattered in Organ Pipe, especially in the Ajo Mountains.

Western and southern Arizona, southern New Mexico, west Texas, Sonora, and Chihuahua, and in California probably adventive.

Spermolepis lateriflora (segregated from *S. echinata* by Nesom 2012) is similar to *S. echinata* in its fruits densely echinate-bristly with uncinate hairs but distinct in its sessile umbels (Nesom 2012). The two species are allopatric, with *S. echinata* occurring from Texas eastward in se USA and in northeastern Mexico.

Figure 39. *Spermolepis lateriflora*. (A) Engineer Canyon, Burro Mts, NM, 12 Apr 2008; (C) Sycamore Canyon near Cliff, Grant Co., NM; photos by Russell Kleinman (gilaflora.com). (B) Texas Canyon, Organ Mts, NM, 15 May 2010, photo by Patrick Alexander (SEINet).

OP Alamo Canyon, *Nichol* 26 Mar 1939. Washes near Sonoyta Hills, 10 Apr 1941, *McDougall 69* Arch Canyon, 2800 ft, 5 Apr 1978, *Bowers 1192*. Gunsight Hills, *Rutman 4 Apr 1998* (ORPI). N-central Puerto Blanco Mts, *Rutman 7 Apr 1998* (ORPI). Santa Rosa Mts, foothills, 2 Apr 2003, *Rutman 2003-446* (ORPI).

CP Daniels Arroyo at Charlie Bell Rd, 10 Apr 1993, *Felger 93-360*

Figure 40. *Yabea microcarpa*. Bull Pasture, 7 Mar 2014.

Yabea microcarpa (Hooker & Arnott) Koso-Poljanski
[*Caucalis microcarpa* Hooker & Arnott]
False carrot. Figure 40.

Small, cool-season annuals, with hispid hairs, and similar to the more widespread *Daucus pusillus*. Leaves finely divided into thread-like or linear segments. Flowers in rather open umbels,

minute, with white petals. Fruits ellipsoid, the body 5–6.5 mm long, with hooked (but not barbed) spines.

Organ Pipe in the Ajo and Bates Mountains, especially at higher elevations.

Western North America from Baja California and Sonora to British Columbia, Idaho, and New Mexico.

OP: N slope Bates Mts, 18 Mar 1944, *Clark 11405* (ORPI). Saddle between Boulder and Arch Canyons, 3800 ft, 3 May 1978, *Bowers 1288a* (ORPI). Estes Canyon, N-exposure, *Wirt 1 Apr 1990*. Crestline of Ajo Mts, 26 Mar 2005, *Rutman 20050326-1*.

APOCYNACEAE – Dogbane Family (includes Asclepiadaceae)

Perennials herbs, vines, or shrubs (in the flora area), many with milky sap. Leaves mostly opposite. Flowers radial, 5-merous, and insect-pollinated. Fruits mostly many-seeded (few seeded in *Matelea parvifolia* and *Metastelma*), the seeds bearing silky hairs and wind-borne.

1. Stems erect or spreading, not vining or twining.

   2. Sap conspicuously milky; flowers green and white to cream or pinkish; fruits mostly ovoid (narrower in *A. albicans* and *A. subulata*), more than 5 mm wide. ..... **Asclepias**
   2. Sap not milky; flowers bright yellow, fruits long and slender, less than 2 mm wide. ..... **Haplophyton**

1. Stems vining or trailing, not self-supporting.

   3. Leaf blades arrow-shaped or broadly heart-shaped, often less than twice as long as wide. ..... **Matelea**
   3. Leaf blades linear to lanceolate, more than twice as long as wide, rarely very narrowly arrow-shaped.

      4. Stems glabrate or sparsely pubescent with scattered, straight hairs; flowers more than 5 mm wide, the corolla rotate with surfaces readily visible. ..... **Funastrum**
      4. Stems with a longitudinal line of usually curved hairs between the nodes; flowers less than 4 mm wide, the corolla campanulate with the inner surfaces of lobes obscured by hairs. ..... **Metastelma**

Asclepias – Milkweeds

Perennials; the stems not vining. Flowers in umbellate clusters. Corolla lobes often reflexed and obscuring the calyx. Fruits linear to broadly ovoid. Seeds many, flat, lightweight, with silky hairs at the apex.

Like many other asclepiad genera, the pollen is massed into paired pollinia (waxy, sac-like structures) joined by a wishbone-shaped translator arm to a corpusculum. The corpusculum may be engaged by the leg, hair, or tongue of an insect, which in its search for nectar carries the pollinium to another flower. Pollination is achieved when an insect visits another flower and inadvertently inserts the pollinium into the slit between adjacent anthers. Wasps (spider wasps, tarantula hawks) and bees seem to the be the primary pollinators in the flora area. Orchids are the only other plants with similarly complex pollinaria.

1. Leaves ovate, at least 2 cm wide.
   2. Plants often more than 1 m tall; leaves sessile, the margins minutely ragged. ... **Asclepias erosa**
   2. Plants usually less than 0.4 m tall; leaves petioled, the margins entire. **Asclepias nyctaginifolia**

1. Leaves linear, less than 2 mm wide (leaves long-lived or quickly deciduous and the stems thus often leafless).

   3. Stems brown, not succulent, not reed-like; leaves more or less persistent, alternate, and very close together, the internodes shorter than the leaves. ..... **Asclepias linaria**
   3. Stems whitish or bluish green, semi-succulent and reed-like; leaves sparse, opposite, and quickly deciduous, the internodes longer than the leaves; reed-stem milkweeds.

      4. Stems usually relatively few (or sometimes as many as 50), usually 1.5–3 m tall; flowers 8–9 mm long (including the down-turned petals), the hoods 2–2.5 mm long and not taller than the fused anthers. ..... **Asclepias albicans**
      4. Stems many, usually to 1–1.5 (2) m tall; flowers 15–20 mm long (including the down-turned petals), the hoods 6–10 mm long and obviously taller than the fused anthers. ..... **Asclepias subulata**

Figure 41. *Asclepias albicans*. (A) Southern Cabeza Prieta Mts, 16 Jan 2005. Plant grown from seed from Cabeza Prieta Mts. (B) 6 May 2005; (C) 14 Aug 2014.

Asclepias albicans S. Watson
White-stem milkweed; *jumate, candelilla*. Figure 41.

Several or more slender, erect, semi-succulent stems to 3 m tall. Leaves few, linear and very quickly deciduous. Umbels 1 to several per stem, from the upper nodes. Flowers cream-white, often suffused with pink, with age turning pale yellowish; corolla lobes 6–7 mm long, the hoods 2–2.5 mm long. Fruits 7.5–15 cm long. Flowering during warmer months.

Arid and exposed, sparsely vegetated rocky hillsides and mountain slopes in Cabeza Prieta and Tinajas Altas, and occasionally on sandy-gravelly soils of bajada-plains along the east side of the Tinajas Altas Mountains. It has been in the Tinajas Altas region for at least 8600 years.

Southeastern California, western Arizona, both Baja California states, and northwestern Sonora.

It is amazing to see these strange slender wand-like stems waving in hot winds on dry slopes, with big orange and black tarantula hawks (spider wasps) clinging to the bobbing flower clusters. The young stems and inflorescence branches of *A. albicans* and *A. subulata* are often covered with yellow aphids (*Aphis nerii*, the oleander aphid, native to the Old World and now widespread). Bright red nymphs and the black and red adults of the small milkweed bugs (*Lygaeus kalmi*) feed on the both reedstem species. *Asclepias albicans* has fewer and taller stems than *A. subulata*, but young plants are often many-stemmed like those of *A. subulata*.

CP: 3 mi W of Tule Well, 1 Apr 1976, *Engard 912* (ASU). Tule Tank drainage, 23 Mar 1992, *Harlan 119* (CAB). Childs Mt, 9 Apr 1993, *Felger 93-300*. Eagle Tank and Buckhorn Tank, 13 & 14 Jun 1992, *Felger* (observations).
TA: Tinajas Altas, 27 Mar 1932, *Shreve 5941*. †Butler Mts, twigs, 3820 & 8570 ybp. †Tinajas Altas, 1230 to 5080 ybp (3 samples).

Asclepias erosa Torrey.
Giant sand-milkweed, desert milkweed; *hierba del cuervo*. Figure 42.

Plants robust, often 1–2+ m tall, with copious milky sap, the stems single or multiple from a perennial caudex with a stout, fleshy taproot. Herbage and inflorescences white woolly when young, glabrate with age. Leaves mostly 13–23 × 9.5–13 cm, broadly ovate below to ovate-lanceolate above, nearly sessile, thick and firm, the midrib and lateral veins prominent, the margins thickened and ragged (erose). Sepals green and pubescent; corollas 8–9 mm long, greenish white, the hoods 4–5 mm long, white. Fruits 5–8 cm long. Growing from winter to early summer; flowering mostly late spring and sometimes in early summer.

Widely scattered, usually as small, localized populations in washes and sand flats in the southwestern part of Cabeza Prieta and westward in southwestern Arizona and adjacent extreme northwestern Sonora.

Also Baja California, southeastern California, southern Nevada, southwestern Utah, and western Arizona.

Flowers visited by large orange and black spider wasps (*Pepsis* and *Hemipepsis*), large yellow-banded tiphiid wasps, and hairstreak butterflies. The wasps can be seen avidly drinking floral nectar in the hot sun. Many orange and black milkweed bugs (*Lygaeus* and *Oncopeltas*) are invariably present, often sucking from unripe fruits, and the flower clusters are often visited by numerous ants tending yellow aphids. It is amazing to find this rather large plant with its large leaves in full flower in intense heat of early summer when almost all other herbaceous plants are dormant or have perished. Does this milkweed grow from a large underground water-storage tissue, and/or do the roots penetrate deeply in the desert sand?

Figure 42. *Asclepias erosa*. (A) Mohave Valley, Mohave Co., AZ, 19 May 2011, photo by Ries Lindley; (B) Calico Basin, W of Las Vegas, NV, May 2005, photo by Stan Shebs (commons.wikimedia.org).

CP: Tule Well, 16 Jun 1992, *Felger 92-622*.
TA: Lechuguilla Desert, *Simmons 21 May 1965*. Camino del Diablo at 0.3 mi W of Cabeza Prieta boundary, 29 Nov 2001, *Felger* (observation).

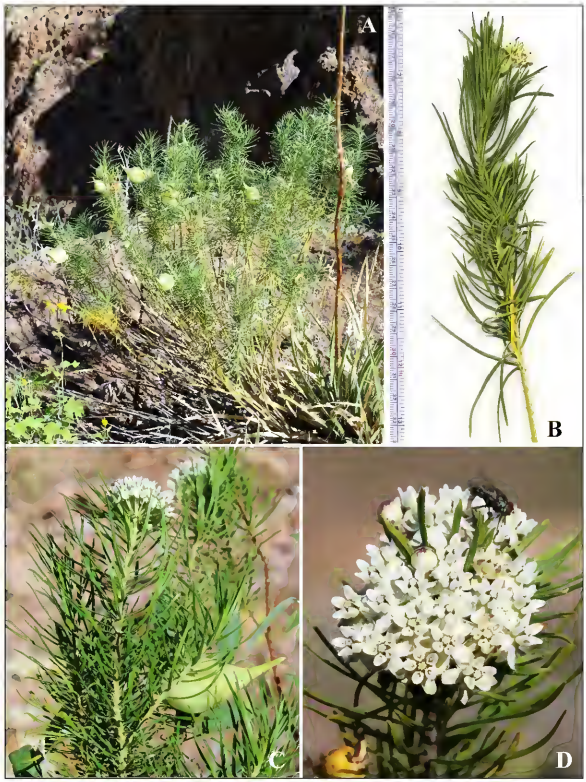

Figure 43. *Asclepias linaria*. (A & B) Estes Canyon, along trail to Bull Pasture, 25 Sep 2013; (C) Arch Canyon, 12 Sep 2013; (D) trail to Bull Pasture, 10 Apr 2005.

Asclepias linaria Cavanilles
Narrow-leaf milkweed. Figure 43.

Small shrubs. Leaves crowded towards the stem tips, sessile, needle-like, about 1 mm wide. Umbels borne near the stem tips. Flowers small, white and pale pinkish, corolla lobes 4–5 mm long. Fruits 3–6 cm long. Growing and flowering with warm weather.

Higher elevations in the Ajo/Diablo mountain complex; scattered and generally on rocky

slopes and drainages. This population is the westernmost for this widespread species and a notably isolated population stranded on an ecological island.

Southern Arizona at elevations above the desert and mountains through much of Mexico except the Baja California Peninsula.

OP. Pitahaya Canyon, *Nichol 23 Feb 1939*. Alamo Canyon, 3000–3800 ft, 31 Mar 1948, *Darrow 3856*.

Figure 44. *Asclepias nyctaginifolia*. Wash bed near N boundary of Organ Pipe & Hwy 85, 14 Aug 2013.

Asclepias nyctaginifolia A. Gray
Mojave milkweed. Figure 44.

Herbaceous perennials from a thick and deeply buried rootstock, dying back in drought or following freezing weather, and new shoots emerging in early spring or summer. Herbage pubescent. Stems spreading or upright. Leaves petioled, the blades relatively thick, dark green, often with reddish veins, and with a wavy (undulate) surface, 3–12 cm long, broadly lanceolate to ovate. Flowers greenish, the corolla lobes 12–15 mm long, the fresh coronas white (becoming yellowish to orange with age). Fruits 5–9 cm long. Flowering in April and with summer rains.

Widely scattered and sometimes locally common across most of Organ Pipe, mostly along washes in valley plains and on hillsides.

Southeastern California and southern Nevada to New Mexico and northern Sonora.

OP. Just N of Mile Post 6, Puerto Blanco Drive, 1723 ft, *Beale 26 Mar 1988* (ORPI). Armenta Well, *Wirt 10 Aug 1990*. Cherioni Wash, ca. 1 mi W of Hwy 85, *Rutman 6 Jun 1998* (ORPI). Cipriano Hills near Pozo Nuevo Road, *Rutman 30 Aug 2001* (ORPI).

Asclepias subulata Decaisne

Desert reed-stem milkweed, rush milkweed; *jumete, candelilla*. Figure 45.

Stems many, slender, semi-succulent and erect, mostly 0.8–1 m tall. Leaves narrowly linear, 1.5–4+ cm long, 0.5 mm wide, few, and quickly deciduous. Umbels 1–several per stem, from upper nodes. Flowers waxy, cream (fading yellowish), the corolla lobes 9–11 mm long, the hood 7–10 mm long. Fruits 8.5–15 cm long. Flowering profusely at various seasons; often one of the few (or the only) plants flowering in late May and June, especially in roadside habitats. Flowers frequented by the large orange-winged tarantula hawk wasp (*Hemipepsis* sp.) and at least one other spider wasp (*Pepsis thisbe*).

Mostly on sandy soils, widely scattered and generally uncommon in the flora area, often solitary or with a few nearby plants. Rare in the southwestern part of Organ Pipe, and slightly more numerous in the southern part of Cabeza Prieta, and occasional in the Lechuguilla Valley of Tinajas Altas region. Common in nearby northwestern Sonora.

Figure 45. *Asclepias subulata*. (A) Dunes S of Sierra Blanca, Pinacate Reserve, Sonora, 17 Feb 2008. Plant grown in Ajo from seed collected along MEX Hwy 8, S of Sierra Blanca. (B) 14 May 2006, (C) 14 Aug 2013.

Grossly similar to *A. albicans* but with shorter, more numerous, and greener stems, and larger and differently shaped flowers. The two species are closely related (Fishbein et al. 2011).

Western Arizona, southern Nevada, and southeastern California to southwestern Sonora and Baja California Sur.

OP: 1 mi N of Quitobaquito, roadside, 13 Sep 1978, *Bowers 1538* (ORPI). 0.5 mi E of Aguajita Wash, North Puerto Blanco Road, *Rutman 28 May 1996* (ORPI)

CP: Las Playas, 24 Nov 1994, *Harlan 447*. S of Jose Juan Tank, in wash, *Balaban 26 Jun 1996* (CAB). Observations: Camino del Diablo 0.8 mi E of W Boundary of Refuge, 29 Nov 2001, *Felger & McCasland*, 9.3 mi E Pinta Sands on Camino del Diablo, 28 Nov 2001, *Felger*.

TA: Camino del Diablo, SE of Raven Butte, 25 Oct 2004, *Felger 04-03*.

Funastrum hartwegii (Vail) Schlechter

[*F. cynanchoides* (Decaisne) Schlechter var. *hartwegii* (Vail) Krings. *F. heterophyllum* (Engelmann) Standley. *Sarcostemma cynanchoides* Decaisne subsp. *hartwegii* (Vail) R.W. Holm]

Climbing milkweed; *gütrote*. Figure 46.

Vines twining into shrubs and trees, sometimes climbing up saguaros or sprawling across the ground; larger individuals in favorable habitats tend to have moderately woody, or corky, basal stems, and other individuals may be herbaceous perennials and not woody or corky. Stems dying back during drought. Crushed herbage and even lightly brushed plants are strongly malodorous. Herbage glabrate or sparsely pubescent. Leaves 3–15 cm long, linear to narrowly triangular, often hastate or sagittate at the base, with one or more yellow-brown conical glands (colleters; drying brown) 0.2–0.4 mm long on upper leaf blade surface at the midrib base. Leaves drought deciduous, leaving long leafless stems trailing and twining along wash bottoms and on vegetation. Flowers maroon and white; corollas 5.5–7.5 mm wide, maroon and white, the margins ciliate; corona and vesicles white. Flowering at various seasons. Fruits 6.5–8.5 cm long, elongated (fusiform) and smooth.

Widespread across lowland areas, foothills, and lower mountain slopes; mostly along washes, especially major arroyos, and also in rocky places. Surprisingly, it even ranges in the hyperarid Butler Mountains west of the Tinajas Altas Mountains.

Central Mexico to southwestern United States.

The sap was widely used by the Hia-Ced O'odham as chewing gum (Philip Salcido & Delores Lewis in Felger et al. 1992). "Set it on the fire and it would become tacky and we would chew it ... has a milky sap ... gather it and heat it up and add water and it becomes white and we chew it" (Betty Melvin in Zepeda 1985: 48, 76). The fresh flowers are marginally edible with an onion-like flavor (Felger & Moser 1985).

OP: Bates Well, *Nichol 26 Apr 1939*. Alamo Canyon, 2000 ft, *Tinkham 18 Apr 1942*. Growler Mts, 16 Apr 1953, *Parker 7982*. Quitobaquito, 14 Sep 1988, *Felger 88-453*.

CP: Monreal Well (Simmons 1966). Buck Mt, *Duncan 28 Mar 1970* (CAB). Papago Well, 20 Mar 1992, *Harlan 45* (CAB). Eagle Tank, Little Tule Well, 12 & 13 Jun 1992, *Felger* (observations).

TA: Tinajas Altas, *Van Devender 9–10 Mar 1980*. Butler Mts, *Van Devender 27 Mar 1983*. Coyote Water, 25 Oct 2004, *Felger 04-46*.

Figure 46. *Funastrum hartwegii*. (A) Little Ajo Mts, 7 May 2006; (B) Kuakatch Wash E of Hwy 85, 10 Sep 2013; (C) Alamo Canyon, 7 Apr 2005; (D) Ajo, 21 Mar 2008.

Haplophyton cimicidum A. de Candolle var. **crooksii** L.D. Benson
[*H. crooksii* (L.D. Benson) L.D. Benson. *H. cinereum* (A. Richard) Woodson. *Echites cimicidus* Pavón ex de Candolle. *E. cinereus* A. Richard]
Cockroach plant, *hierba de la cucaracha* Figure 47.

Spindly to bushy perennials with very slender straight stems. Leaves drought deciduous,

opposite and/or alternate especially above; petioles short, the blades lanceolate, thin, often ca. 2–3 cm long. Flowers bright yellow and showy, the floral tube ca. 1 cm long; flowering at various seasons following rainfall, mostly summer–fall. Capsules paired, 6–10 cm long and very slender–2–2.5 mm wide; seeds black with a tuft of hairs at each end.

Figure 47. *Haplophyton cimicidum*. (A) Upper San Pedro River floodplain, Charleston Hills, Cochise Co., 8 Sep 2002, *Makings 1341* (ASU). (B–D) Alamo Canyon above the well, 7 Feb 2013.

Ajo and Puerto Blanco Mountains, generally on north-facing slopes in protected places, canyons, and at higher elevations.

Southern Arizona to west Texas and southward to Guatemala (reports from the Caribbean are based on the dubious location of the type of *H. cinereus*). The plant has been used as an insecticide in Mexico, hence the common name. In 1942 Benson described the northern populations as var.

crooksii in southern Arizona and northern Sonora, differentiated mostly by smaller leaves and seeds, and seed surfaces with some difference in ornamentation. One year later he recognized the variety as a distinct species. Williams (1995) presents a case for recognizing the two taxa at the species level, citing differences in seed size, color, and ornamentation, corolla aestivation, and an apparent disjunction in the distribution in Mexico (but with all Sonoran populations attributed to the northern taxon). The Sonoran Desert populations have smaller leaves than those beyond the desert in southern Sonora, which overlap considerably with southern Mexican populations in the diagnostic traits cited by Williams (1995).

OP: Estes Wash in side canyon, 20 Aug 1950, *Supernaugh 432*. Side canyon of Grass Canyon, 12 Sep 1978, *Bowers 1516*. Arch Canyon (NE of the arch), *Wirt 30 Sep 1989* (ORPI). Puerto Blanco Mts, foothills of Pinkley Peak, 31 Oct 2003, *Rutman 20031031-33*

Matelea

Vines, the herbage foul-smelling when crushed. Leaves opposite, the leaf blade bases cordate or sagittate. Corona a deeply 5-lobed ring. *Matelea* is polyphyletic and very heterogeneous. (Mark Fishbein, pers. com. to Richard, Jan 2013).

1. Leaves 2–10 cm long, thin and broadly heart-shaped (cordate); flowers cream; fruits smooth, more than 8 cm long. ..... **Matelea cordifolia**
1. Leaves less than 2 cm long, somewhat thick and arrow-shaped; flowers brownish or greenish; fruits less than 6 cm long, with few, short tubercles. ..... **Matelea parvifolia**

Matelea cordifolia Woodson
[*Rothrockia cordifolia* A. Gray]
Heart-leaf milkweed vine. Figure 48.

Woody-based vines with corky bark growing through desert shrubs and trees, densely pubescent, with long straight hairs and shorter glandular hairs. Leaves drought deciduous, long petioled, the blades to 10+ cm long, thin and more or less heart shaped. Corollas about 15 mm long, lobed nearly to the base, cream-colored and faintly lined, the corona mostly hidden within the corolla tube, green. Fruits about 10 cm long, elongated, smooth, mottled green and whitish. Flowers, fruits, and foliage produced at various times of the year following rainy periods except during the coldest weather.

Known from the United States only in canyons in the Ajo and Diablo Mountains and from the type collection in Arizona in 1884, probably in mountains near Tucson. It has not been recorded in the Diablo Mountains since the 1951 collection. Sue Rutman (2014) reports, "I've looked for but never found any *Matelea cordifolia* in Diablo Canyon, where Supernaugh found it. I found a single non-reproductive plant in Alamo Canyon in 1996. It remained non-reproductive through 2002, but has not been seen since. I suspect that the deep drought of 2002 killed it." It does, however, occur in Sonora near the southeastern part of Organ Pipe.

Mexico in Sonora, Isla Tiburón, and Baja California Sur.

OP: Canyon Diablo, 15 Apr 1951, *Supernaugh 440* (ORPI). Alamo Canyon, *Rutman 9 Apr 1996* (ORPI).

Sonora: Mpio General Plutarco Elías Calles, Sierra Cubabi (SE of Sonoyta), N-facing drainage at middle elevation, [31 72143°N, 112 82064°E in SEINet], 700 m SE of highest point in area, 1130 m, granite with *Stenocereus thurberi, Justicia californica, Fouquieria splendens, Simmondsia chinensis, Ferocactus covillei, Eriogonum wrightii, Encelia farinosa*, woody vine growing up through *Vauquelinia californica*, 19 March 1991, *Baker 8131* (ASU).

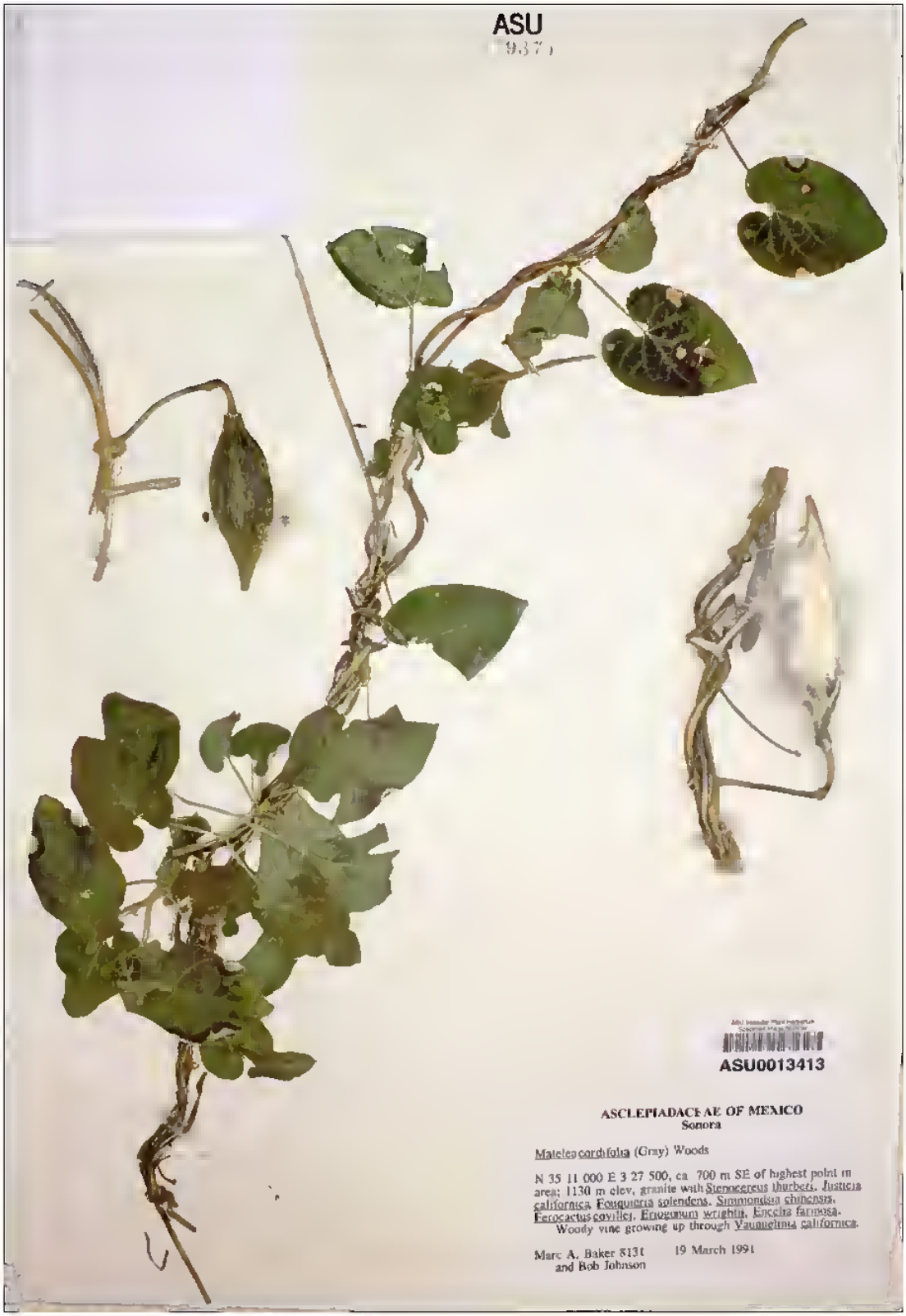

Figure 48. *Matelea cordifolia*. Sierra Cubabi, Sonora, 19 Mar1991, *Baker 8131* (ASU, from SEINet).

Matelea parvifolia (Torrey) Woodson
Spearleaf milkweed vine. Figure 49.

Small perennial vines, pubescent but not glandular, the hairs curving downward. Leaves less than 2 cm long, dull green, somewhat thick, ovate to arrow-shaped (triangular-lanceolate). Flowers greenish to dark brown-purple, 5 mm long. Fruits mostly less than 6 cm long, slender with few short, blunt tubercles.

Widespread and easily overlooked, on rocky slopes through much of Organ Pipe including the Ajo Mountains and localized in washes at the northeastern corner of Cabeza Prieta.

Southeastern California to Arizona, Trans-Pecos Texas, and adjacent northern Mexico.

Figure 49 *Matelea parvifolia*. (A) Victoria Mine area, 12 Sep 2013; (B) bajada S of Ajo Mts, 2 Mar 2008.

OP. Near mouth of Alamo Canyon, *Mulroy 2 May 1970*. Bull Pasture, 2 May 1978, *Bowers 1272* (ORPI). Grass Canyon, 9 Dec 1978, *Bowers 1515*. Foothills, NW part of Puerto Blanco Mts, 7 Mar 2002, *Rutman* (observation)

CP. Charlie Bell Rd, 1.9 km NE of Little Tule Well, 5 Mar 1994, *Felger 94-29*.

Figure 50. *Metastelma arizonicum*. (A) Middle fork of Alamo Canyon, 24 Mar 2008, (B) trail to Bull Pasture, 21 Sep 2008; (C) Arch Canyon, 14 Sep 2013.

Metastelma arizonicum A. Gray

[*Cynanchum arizonicum* (A. Gray) Shinners. *Metastelma watsonianum* Standley]. Figure 50.

Small vines with many slender stems often twining together, often growing on small shrubs, or the stems sometimes vining on themselves and the plants forming small bushes. Plants glabrous except stems having with a longitudinal line of hairs between the nodes, the hairs short, white, and often recurved, and also with a similar line of hairs along the upper leaf midrib. Leaves 1.2–3 cm long, short-petioled, the blades narrowly oblong, dark green in winter, the margins becoming inrolled (revolute) especially in dry seasons. Flowers 4 mm long, in small axillary clusters, the petals (at least adaxially), corona, and gynostegium are all cream white. Inner surface of the corolla lobes densely hairy with white villous hairs. These hairs point downward towards the center of the flower—a small insect attracted to the flower would be directed towards the center of the flower, and the downward pointing hairs would prevent its access elsewhere. Fruits 4.5–6 cm long, elongated and smooth.

Arroyos, canyons, and rocky slopes; widespread in Arizona Upland regions of Organ Pipe, especially in the Ajo and Puerto Blanco Mountains.

Central Arizona to northern Sinaloa.

OP: Ajo Mts, "Sierra de Alamos," *Nichol 16 May 1937*. Dripping Springs, 18 Mar 1945, *Darrow 2456*. Bull Pasture Trail, 5 Nov 1977, *Bowers 947*. Walls Well Rd, *Van Devender 30 Aug 1978*. Upper North Alamo Canyon, 7 Mar 1987, *Van Devender 87-3*.

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YUCCA FREEMANII (ASPARAGACEAE) NEW TO ARKANSAS

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ABSTRACT

Yucca freemanii is documented from Arkansas and is recognized as a component of the vascular flora of Arkansas. In June and July 2014, the collection site was visited by Craig Frasier and a *Yucca* of unknown identity was photographed. The authors then collected herbarium specimens (including flowers in liquid preservative) and sterile rosettes/rhizomes for growth in a *Yucca* common garden. The plants at this site differ from populations of *Y. louisianensis* in southwestern Arkansas that have been under study for several years and are consistent with those of Shinners' description of *Y. freemanii*, a type specimen observed online, and herbarium specimens examined previously. Based on these data, we recognize *Y. freemanii* as a valid taxon and new to the Arkansas flora.

Shinners (1951) described *Yucca freemanii* from a specimen collected by H.A. Freeman in Bowie County, Texas, in 1950 and attributed the species to Texas and Louisiana based on specimens at Southern Methodist University (SMU) and the Missouri Botanical Garden (MO). Since its initial description, *Y. freemanii* has received diametrically opposed treatments from taxonomists, ranging from a valid species (Correll & Johnston 1970) to a synonym of *Y. flaccida* Haw. (Hess & Robbins 2002) or *Y. louisianensis* (Diggs et al. 2006). Diggs et al. indicated that until a thorough study was made of the complex of *Yucca* species in east Texas, they were following various authors in using *Y. louisianensis* for the common species of *Yucca* in east Texas and were including *Y. freemanii* within *Y. louisianensis*. They also noted that Shinners separated *Y. freemanii* from *Y. louisianensis* based on its glabrous inflorescences as well as other differences.

On 26 June, 29 June and 6 July 2014, the site of collection was visited by Craig Frasier to photograph an assemblage of rare species noted by Theo Witsell in a previous visit. During this visit, a *Yucca* of unknown identity was photographed (Figs. 3, 4, 5). Frasier shared digital images with Theo Witsell, who shared the images with the second author and Matt White. The second author determined that the plants mostly closely matched *Y. freemanii*, a taxon generally not recognized by taxonomists and not previously reported for Arkansas (Gentry et al. 2013). The site was visited by the authors on 20 July 2014, and the plants were re-photographed, herbarium specimens were collected (including flowers in liquid preservative), and sterile rosettes/rhizomes were collected for growth in Johnson's *Yucca* common garden (Figs. 2, 6). Character states of the plants at this site are consistent from plant to plant and are different from nearby populations of *Y. louisianensis* that have been under study by Johnson for several years. Also, the character states of the plants at the collection location are consistent with those of Shinners's description of *Y. freemanii* (Shinners 1951), an isotype of *Y. freemanii* observed online at TROPICOS (MO 1703856 & MO 1703857) (Tropicos 2014), and specimens identified as *Y. freemanii* previously examined by Johnson at BRIT (*Van Vleet 1631*) and also listed by Shinners (1951) as an example of *Y. freemanii*. There is no evidence that these plants are the result of hybridization/introgression or are the result of an escape from

cultivation. Based on these data, we recognize *Y. freemanii* as a valid taxon and new to the Arkansas flora.

Voucher specimens. **ARKANSAS**. Miller Co: Ravanna 7.5' Topo. Quad (AR-TX-LA), extreme sw Miller County, near LA and TX state lines, two small populations of plants growing in Bowie Series Soil (sandy loam), few flowers remaining on plants, leaves yellowish-green, thick, flaccid and somewhat succulent, inflorescence bright green, glabrous, thin-stemmed, with a hard and almost smooth surface, flowers greenish-white, nearly globose, small, ca. 3.0 cm long, growing with *Pteridium aquilmum, Toxicodendron radicans*, and *Physostegia digitalis*, 20 Jul 2014, *G.P. Johnson 5945A,B,C,D* (APCR). Rosettes A & B: along Co. Rd 1, 1.1 km SE of Ravanna, 33.05215° N, -94.03046° W, +/- 3m, 60 m elev., NW 1/4 of NE 1/4 of Sect. 5, T20S, R28W, powerline right-of-way on E side of road, flat area between ditch and cut-over woods edge. Rosettes C & D: along Co. Rd 1, 157 m NW of intersection with Co. Rd 80, 33.04568° N, -94.02663° W, +/-3m, 69 m elev., NE 1/4 of SE 1/4 of Sect. 5, T20S, R28W, powerline right-of-way on E side of road, flat area between ditch and pine stand.

These plants of *Yucca freemanii* occur in two populations at opposite ends of a 1 km segment of County Road 1 (Fig. 1). At both locations, the plants occur in a Bowie Sandy Loam Soil (Laurent 1984) at the highest point topographically. Due to the clonal nature of *Yucca*, what has been observed before in other stemless *Yucca* seems to be true for *Y. freemanii* — what appears to be a large number of individual plants above ground are actually one or a few plants whose rosettes are connected below ground by an extensive "woody" rhizome system. When the plants were collected for herbarium specimens and dug as rosettes/rhizomes for a *Yucca* common garden, there was an extensive rhizome system and rosettes of various sizes (and ages?) and distances from each other were all connected below ground. This would also account for the uniformity of character states within the plants. As is unfortunately often the case in *Yucca*, while flowers were abundant this year in each population, fruit formation was absent, presumably due to an absence of pollinating moths.

Historically, *Yucca freemanii* has been confused with *Y. louisianensis* (Shinners 1951) and in their area of sympatry in northeast Texas has been recently treated as a synonym of it (Diggs et al. 2006). Diggs et al. noted that individuals of *Y. louisianensis* with glabrous inflorescences are occasionally found and that these were recognized as *Y. freemanii* by Shinners; they also noted that Shinners recognized other differences between *Y. freemanii* and *Y. louisianesis*. As has been mentioned by many authors, real differences between *Yucca* taxa are often difficult if not impossible to see in herbarium specimens. And while Shinners' description of *Y. freemanii* is excellent, until the species is seen in the field and compared directly to living plants of *Y. louisianensis* (Fig. 7), those differences cannot be fully appreciated, especially in herbarium specimens. As called for by Diggs et al. (2006) and Smith (1988), the first author (Johnson) is making a field, herbarium and nomenclatural study of *Yucca* in the southeastern USA, including the Arkansas-Louisiana-Texas area, and keys, descriptions, and nomenclature for the taxa of *Yucca* recognized will be forthcoming. Until that time, the key in Shinners (1951) will separate *Y. freemanii* from *Y. louistanensis*.

1 Leaf margins minutely toothed or smooth, not shredding ..... **Yucca pallida** McKelvey
1 Leaf margins shredding into prominent white threads (these often largely disappearing late in the year)

2 Inflorescence spicate-racemose, occasionally with 1–2 branches near base, borne close to or even partly below the summit of the leaves, plant 0 6–1 2 m high, flowering late April-mid May ..... **Yucca arkansana** Trel.
2 Inflorescences panicled, with branches in more than half its length, elevated well above the leaves, plant 1–4 m high, flowering late May-July.

3. Panicle branches glabrous, scape 1–1.8 m high, slender (4–5 mm thick at base of inflorescence), leaves 1–4 cm wide, broadly acute or subacuminate, rather soft and limp, flowering mid June-July ..... **Yucca freemanii** Shinners

3. Panicle branches densely pubescent, scape 1.5–4 m high, stout (5–10 mm or more thick at base of inflorescence), leaves 0.4–2 cm wide, narrowly acute or acuminate, rather firm and stiff, flowering late May-June (sporadically later) ..... **Yucca louisianensis** Trel.

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We gratefully acknowledge Theo Witsell and Matt White for their contributions to this paper. Although he did not see *Yucca freemanii* there, Theo Witsell discovered this site and directed Craig Frasier to it as a location for photography of several species of rare plants. Matt White examined the first digital photographs taken of the site by Craig Frasier and concluded that the *Yucca* seen in the photographs matched *Y. freemanii*, a taxon that he has long considered to be distinct from *Y. louisianensis*.

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Figure 1. *Yucca freemanii* site along Co. Rd 1, Miller Co., Arkansas, 20 Jul 2014. Photo by George Johnson.

Figure 2. Plants of *Yucca freemanii* collected for herbarium specimens/common garden transplantation, Miller Co., Arkansas, 20 Jul 2014. Photo by George Johnson.

Figure 3. Immature inflorescences of *Yucca freemanii* behind *Physostegia digitalis* and *Pteridium aquilinum*, Miller Co., Arkansas, 26 Jun 2014. Photo by Craig Frasier.

Figure 4. Mature flower of *Yucca freemanii*, Miller Co., Arkansas, 6 Jul 2014. Photo by Craig Frasier.

Figure 5. *Yucca freemanii* whole plant with basal rosette, inflorescence and flowers in bud, Miller Co., Arkansas, 29 Jun 2014. Photo by Craig Frasier.

Figure 6. Whole plant of *Yucca freemanii* with a few remaining flowers, Miller Co., Arkansas, 20 Jul 2014. Photo by George Johnson

Figure 7. *Yucca louisianensis* in fruit, Miller Co , Arkansas, 20 Jul 2014 Photo by George Johnson

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NEW VASCULAR PLANT COUNTY RECORDS FROM BRONX COUNTY, NEW YORK

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ABSTRACT

The submerged aquatic flowering plant species *Potamogeton pusillus* (small pondweed) and *Potamogeton foliosus* (leafy pondweed) are reported from Bronx County, New York, for the first time.

A team from The New York Botanical Garden, the Bronx River Alliance, and the New York City Department of Parks and Recreation surveyed the upper reaches of the Bronx River in August 2014, looking for native and invasive species of submerged aquatic plants. The survey was jointly organized by NYC Parks, NY-NJ Harbor & Estuary Program, the Bronx River Alliance, and representatives from other federal, state, city, university, and community organizations.

Survey methods involved visual inspection from canoe and kayak, collection of herbarium and DNA samples, and detailed data collection, including GPS coordinates, habitat, and plant descriptions. All species were vouchered with herbarium specimens and DNA samples that will be archived in the Garden's William and Lynda Steere Herbarium and publicly available on the internet through the C.V. Starr Virtual Herbarium (2014).

Between Shoelace Park at 219th St and Southern Boulevard, just north of the Garden, the team discovered six species of submerged aquatic flowering plants, four native and two exotic. Two of the native species found, horned waterweed and common pondweed (*Zannichellia palustris* and *Elodea canadensis*, respectively), were documented from the river in 2010 within The New York Botanical Garden and were suspected in this section of the river as well. The other two native species found, small pondweed (*Potamogeton pusillus*) and leafy pondweed (*Potamogeton foliosus*), have never been documented from the river before and are new records for Bronx County. The team also found one small population each of the alien species pond water-starwort (*Callitriche stagnalis*, *Atha et al. 14843*, NY) and curly pondweed (*Potamogeton crispus*, *Atha et al. 14846*, NY).

The discovery of a diverse assemblage of native species thriving in the waters of the Bronx River are a testament to the hard work and dedication of the many groups and individuals who have worked tirelessly over the years to clean up the Bronx River and make it a vibrant, diverse, and healthy cultural and environmental treasure.

Potamogeton pusillus L.

New York. Bronx Co.: City of New York, Bronx River, between 216th St and 219th St, 40.883251 N, 73.867821 W (±25m), 16 m, fine silt, banks dominated by *Acer saccharimum*, 18 Aug 2014, *Atha, Feliciano, and Felber 14838* (NY).

New York. Bronx Co.: City of New York, Bronx River, at about 213th St, 40.880304 N, 73.868945 W (±25m), 16 m, fine silt, 18 Aug 2014, *Atha, Feliciano, and Felber 14847* (NY).

This species is native throughout North America (USDA 2014) and occurs in both acid and alkaline waters (Gleason & Cronquist 1991).

Potamogeton foliosus Raf.

New York. Bronx Co.: City of New York, Bronx River, between 216th St and 219th St, 40.883251 N, 73.867821 W (±25m), 16 m, fine silt, banks dominated by *Acer saccharinum*, 18 Aug 2014, *Atha, Feliciano, and Felber 14840* (NY).

New York. Bronx Co.: City of New York, Bronx River, at about 213th St, 40.880304 N, 73.868945 W (±25m), 16 m, fine silt, 18 Aug 2014, *Atha, Feliciano, and Felber 14845* (NY).

This species is also native throughout North America except Greenland, Nanavut, Newfoundland, and Labrador (USDA 2014). It occurs in streams and ponds (Gleason & Cronquist 1991).

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A NEW COMBINATION FOR *MONNINA* (POLYGALACEAE)

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ABSTRACT

A new combination for a Colombian species of *Monnina* (Polygalaceae) is made: *Monnina padifolia* (Bonpl.) Freire-Fierro, based on *Hebeandra padifolia* Bonpl. The illegitimate name *Monnina phytolaccifolia* Kunth has previously been used for this species.

Monnina, an herbaceous to arborescent genus endemic to the New World, comprises about 150 species distributed from the southwestern USA (Blake 1924) to the southern Cone of South America (Freire-Fierro & Pastore 2008). As a result of floristic (Freire-Fierro in press) and phylogenetic studies of *Monnina* (Freire-Fierro et al. unpubl. data), it was realized that one of the Colombian species was described earlier in a different genus, *Hebeandra* Bonpl., and I publish here a new combination based on the earlier name.

Monnina was originally described by Ruiz and Pavón (1798). Bonpland (1808), unaware of this name, described 16 species of *Monnina* under his new genus *Hebeandra*. One of these names, *H. padifolia* Bonpl., was used to describe a Colombian species ("prope Hundam"). Bonpland (1808), while describing *H. padifolia*, says that there is also a variety "β" for material collected in Venezuela ("prope Avila").

Kunth (1823) while synonymizing *Hebeandra* under *Monnina*, created several nomenclatural problems grouped into four categories by Eriksen (1996a). One of these categories (i.e., homotypic names with different epithets) is the one that applies to the present problem. According to Eriksen (1996a), Kunth, using the same specimens studied by Bonpland, described the Colombian material as *M. phytolaccifolia* var. "α" and discussed a Venezuelan collection, which appeared to be different than the Colombian material, as *M. phytolaccifolia* var. "β".

Since the legitimate and illegitimate names of Andean *Monnina* published by Kunth had been widely used, Eriksen (1996b) proposed the conservation of the illegitimate names. However, her proposal was rejected (Brummit 1999; Nicolson 1999a, 1999b) and in publishing a treatment of Polygalaceae for Flora of Ecuador, Eriksen et al. (2000) provided the necessary replacement names for the illegitimate names used in Ecuador. An illegitimate name, *M. phytolaccifolia* for the Colombian species has been generally used until now, and I propose the following new combination to resolve this problem.

Monnina padifolia (Bonpl.) Freire-Fierro, **comb. nov**. Basionym: *Hebeandra padifolia* Bonpl., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamten Naturk. 2: 42. 1808. *Monnina phytolaccifolia* (as '*phytolaccaefolia*') "var. α" Kunth in Humboldt & al., Nov. Gen. Sp. [quarto ed.] 5: 413, t. 503. 1823; ibid. [folio ed.] 5: 323, t. 503 (as '*Monna*'), *nom. illeg.* **TYPE: Colombia**. Tolima. Near Mariquita, 760 m, Jun 1801, Bonpland *& Humboldt s.n.* (lectotype designated by Eriksen 1996a: P-00679689!; isolectotypes: B-W 13045 as image!, P-00507007!, US-00109110!).

Monnina padifolia is a Colombian species widely distributed in secondary habitats of montane forests and it occurs between 800 and 3400 m (Freire-Fierro in press).

The Venezuelan collection ("*Monnina phytolaccifolia* var. "β"), a syntype of *M. phytolaccifolia*, that was cited in the protologue, is now recognized as *M. cladostachya* Turcz. (see Aymard & Campbell 2008). This species is only recorded from Venezuela (see Ferreyra 1957; Taylor 1985; Eriksen et al. 2000; Freire-Fierro in press).

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THOMAS WALTER TYPIFICATION PROJECT, VII: OBSERVATIONS ON THE GENUS *COLLINSONIA* (LABIATAE) AND A NEOTYPE FOR *C. SEROTINA* WALTER

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ABSTRACT

Thomas Walter published his *Flora Caroliniana* in 1788. Because of the early date of this flora, many of its species were new to science, and the names given them by Walter remain of importance in the botany of the American Southeast. Walter kept no herbarium, and uncertainty has followed the application of many of his names. Previous numbers of this series have addressed many of these untypified species. Here, attention is given to the species of *Collinsonia* (Labiatae) and particularly to a mint described by Walter, *C. serotina*, whose name has often been disregarded as ambiguous, now made certain by selection of a replacement for the missing type, a neotype. This typification displaces the long-familiar *C. anisata* Sims.

Thomas Walter (1740-1789) was the owner of a rice plantation on the Santee River, Berkeley County, South Carolina. In 1788 he published a small book, *Flora Caroliniana*, a compilation of the plants that he knew within a 50-mile radius of his home. But he also included other species that are unknown on the Carolina coastal plain. In the fall of 1786 he was visited by a Scot, John Fraser, who came to the Carolinas in search of plants of value for English horticulture. Fraser collected widely during 1787, venturing far into Georgia in the company of Andre Michaux, the French botanical explorer, and into the western Carolina mountains. It is believed Fraser brought to Walter plants he would otherwise not have known and included by him in his *Flora*.

But Walter kept no herbarium (Ward 2007a), and a significant number of the names he published are uncertain as to their modern application. An effort, the Thomas Walter Typification Project (Ward 2006, 2007b, 2007c, 2007d, 2008a, 2008b), has published neotypes, lectotypes, and epitypes for many of these questionable names. By the selection of type specimens to represent these names, they become fixed in their meaning, bringing stability to the nomenclature of this portion of the Southeastern flora.

One small genus addressed by Walter contained problems, both of nomenclature and taxonomy, too complex to be summarized in the concise format employed by prior numbers of the TWTP. Walter (1788: 65) named and described two species of *Collinsonia* — *C. praecox* and *C. serotina*. These are mints (Labiatae) of a genus established by Linnaeus (1753: 28). Walter's first species, *C. praecox*, is often treated as a synonym of the type species of the genus, *C. canadensis* L., and is not of issue. His second, *C. serotina*, has been problematic and is untypified. The genus consists of only a few species, and one would think it straightforward to match Walter's description of *C. serotina* with the appropriate plant of the Carolinas.

But previous authors have not found the assignment of Walter's name to be so simple. Well into the 20th century *Collinsonia serotina* was merely listed as a name or more often wholly disregarded as perhaps one of the seven species of *Collinsonia* recognized by Elliott (1816). [Elliott considered Walter's plant to be *C. tuberosa* of Michaux (1803), neglecting the prior date of Walter's publication. His identification was incorrect, as will be shown.]

THE GENUS *COLLINSONIA*

In recent years the genus *Collinsonia* has twice been given significant study, by Shinners (1962) and by Peirson et al. (2006). Shinners considered the genus to consist of four species: *C. verticillata* Baldw. ex Ell., from Tennessee and North Carolina into Georgia; *C. canadensis* L., from Kentucky and Maryland south into panhandle Florida; *C. tuberosa* Michx., from Georgia and Tennessee south into Georgia and Louisiana; and *C. serotina* Walt., from North Carolina south to Florida and west to Louisiana. Peirson et al. also believed the genus to consist of four species, but aligned differently; they recognized *C. verticillata* Baldw. ex Ell., *C. canadensis* L. (incl. *C. tuberosa* Michx.), *C. punctata* Ell. (perhaps incl. *C. serotina* Walt.), and *C. anisata* Sims.

Of these species, *Collinsonia verticillata* is relatively distinct and is treated similarly by Shinners and Peirson et al. Though found in the Carolinas, it was not known by Walter and need not be considered further.

Collinsonia canadensis, as viewed by Shinners, is a rather uniform species with stout stems, large leaves, and small flowers. He distinguished it from *C. tuberosa*, with its slender stems and small leaves; the flowers also are small. [*Collinsonia serotina*/*C. punctata* is readily defined by its relatively large flowers.] Peirson et al., with opportunity to observe these plants both in the field and under cultivation (which Shinners had not), while acknowledging the differences reported by Shinners, found the two entities to form a continuum and were not willing to separate them taxonomically. But insofar as the determinations by Ahles (in Radford et al. 1968) of the differences between *C. canadensis* and *C. tuberosa* are accurate, the former is largely western in the Carolinas, while the latter is exclusively on the coastal plain (including a reported collection from Berkeley Co.). Thus, as far as these two taxa may be distinguished, the plant Walter knew near his home on the coastal plain and named *C. praecox* would have been what has more recently been termed *C. tuberosa*. Where it is desired to distinguish the two, Walter's name being prior (1788 vs. 1803), the small-leaved, small-flowered Carolina *Collinsonia* is correctly known as *C. praecox* Walter. The distribution and comparative morphology of these taxa, however, are yet to be confirmed and appear not to impact the stated purpose of the present study.

COLLINSONIA SEROTINA

With *Collinsonia verticillata* and *C. canadensis* (incl. *C. tuberosa*) resolved or deferred, Walter's *C. serotina* is less obscure. Shinners (1962), as noted, treated *C. serotina* as undivided; he included within it two other names that will show importance later: *C. punctata* Ell. and *C. anisata* Sims. Peirson et al. (2006), in contrast, employed *C. punctata* (or *C. serotina*) and *C. anisata* as distinct species. Both authors noted these taxa to be readily distinguished from *C. canadensis* by their appreciably larger flowers.

The treatment of *Collinsonia punctata*/*C. serotina* by Peirson et al. (2006) contains a confusing internal contradiction and a puzzling misstatement as to typification. In his master's thesis, Peirson was consistent as to nomenclature. But when it came time for publication and his advisors were added as co-authors, there perhaps were too many cooks stirring the pot. In the Abstract and throughout the prefatory discussion, one of the four recognized species was repeatedly termed "*Collinsonia serotina*." Yet in the following key and in the treatment of species, this fourth species became "*Collinsonia punctata*." Between, a paragraph was inserted in which the authors stated that "the name *C. serotina* is hereby rejected as an ambiguous name."

Peirson et al. (2006: 403) further explained the rejection of *Collinsonia serotina* Walt. by asserting that "The specimen in the Walter Herbarium at the British Museum is in poor condition and possesses no floral material; its identity could not be determined with certainty." No source for this claim was cited. Perhaps it was an expansion of Shinners (1963: 78), who stated that "According to Fernald and Schubert (1948), there is a specimen in the Walter Herbarium which is the same as *C. punctata* Elliott."

But Fernald & Schubert (1948) had made no such statement. Their 1948 paper was a well-illustrated report of the findings of Schubert in photographing British type collections. They did discuss *Collinsonia serotina* (p. 223), noting Walter's name to have priority over Elliott's *C. punctata*. But they referred to no specimen in the Walter Herbarium.

In fact, there is no specimen of *Collinsonia* in the Fraser/Walter folio herbarium of the Natural History Museum, London. The specimens in the folio are arranged alphabetically by the names assigned them by Fraser or Walter. On page 35 of the folio, where *Collinsonia* would be expected, spm. 35-E is labeled "*Clitoria*" in Fraser's hand (= *C. mariana* L.) and spm. 35-F is labeled "*Commelina*" in Walter's hand (= *C. erecta* L.). Nor is there an unnamed specimen elsewhere in the herbarium that has been identified as a species of *Collinsonia*.

These vagaries aside, Peirson et al. (2006) emphasized a little-understood detail of floral morphology within the genus *Collinsonia*: the presence in different populations of either two or four stamens per flower. As Shinners (1962) had noted, stamen number in the Labiatae has been used to separate genera and even whole tribes. Yet here, some plants have only two stamens, considered characteristic of typical *Collinsonia*, while others with four stamens have been segregated into the genus *Michelielia* (e.g., Small 1933, as *M. anisata* (Sims) Briq.). This distinction is now agreed to be valueless in separation of genera.

But Peirson et al. (2006) did find correlation of stamen number with quite another feature, that of odor. They reported plants with an anise-like scent reliably to have four stamens and to range from central Georgia to panhandle Florida and west across Alabama to southern Mississippi; plants with a lemon-like scent and two stamens were limited to southwestern Georgia and panhandle Florida to southern Mississippi. [Plants of *C. canadensis* were also found to have a lemon-like scent.] The ranges of these two variants overlapped appreciably, though with some areas exclusive (especially of the anise-scented form). Peirson et al. reported further correlation with a series of morphological variables, sufficient for them to justify separation of *C. punctata* from *C. anisata*.

Peirson's separation of the *C. punctata*/*C. anisata* complex at species level of two populations on the basis of differing scents and differing stamen numbers, even though reported to be correlated with other morphology, is not supported here. Abundant herbarium materials annotated by Peirson could not be reliably distinguished except by floral dissection (and stamen count); odor was not apparent in dried materials. Flower size (if present) was quite satisfactory as a determinant of the complex, with flowers appreciably larger than *C. canadensis*/*C. tuberosa*. There may be room to recognize the two taxa on basis of scent, perhaps at the level of variety or form. But neither flower size nor other morphology was of value in separating *C. punctata* from plants identified by Peirson as *C. anisata*.

Further damaging to the thesis that two species may be recognized within this complex is the fact that none of the names has a clear provenance. *Collinsonia serotina* was described by Walter (1788) without indication of origin. *Collinsonia anisata* was described and illustrated from a plant cultivated in England (Sims 1809), said to be "a native of South-Carolina." *Collinsonia punctata* was a plant apparently known in the field by Elliott (1816) and described in detail; yet its source is unknown and almost its only significant mark is that the flowers had four stamens. By Peirson's distribution maps, there is essentially no likelihood that any plant identifiable by any of these names could have been obtained in the Carolinas. [A single collection marked as *Collinsonia punctata* from Allendale Co., South Carolina, thus disjunct from others of this complex, appears to be *C. canadensis*, frequent in nearby counties.]

Even so, the probable source of Walter's *Collinsonia serotina* and Elliott's *C. punctata* (and perhaps Sims' *C. anisata*) can be deduced. Peirson et al. (2006) mapped a cluster of counties in north-central Georgia where his *Collinsonia anisata* (so annotated) has been collected. Independently, Jones and Coile (1988) mapped their *C. serotina* with the same distribution. Across

these counties was once the Lower Creek Trading Path, the ancient Indian trail from Augusta to the Mississippi River, followed by William Bartram in 1775 and John Fraser in 1787 (Ward 2014), and by Stephen Elliott in 1818 (and earlier?) (to purchase land vacated by the retreating Creeks; Huck 2007). It is a reasonable supposition that it was along this trail that Fraser collected the plant, which was then taken to Walter and named *C. serotina*. And Elliott, following the same path, may have found his *C. punctata*, a plant unknown in his home state. Perhaps even *C. anisata* has a common source, for Fraser is known to have brought to England seeds of many Carolina and Georgia species, for commercial distribution (Britten 1899). [Other species native to this area but absent from the Carolinas were also surely found here by Fraser and were described by Walter: *Delphinium carolinianum* Walt., *Stlene catesbaei* Walt., etc. (Ward 2014).]

TYPIFICATION AND CONCLUSIONS

In the absence of authentic original materials, the International Code of Botanical Nomenclature (McNeill et al. 2006) permits selection of another specimen — a neotype — to represent the missing type. The specimen so selected as neotype for *Collinsonia serotina* Walter should be chosen in belief that it represents the population from which Walter's material may have come. An appropriate specimen is here selected, from a Georgia county traversed by the ancient Indian trail.

Collinsonia serotina Walter, Flora Caroliniana, 65. 1788. **NEOTYPE** (selected here): USA. **Georgia**. Meriwether Co.: Rocky soil, by beaver pond, Fairly common, Pine Mountain trail, 6 Sep 1982, *M.A. Garland 95* (GA; annot. *Collinsonia anisata* Sims, by Peirson in 2002).

Thus, by the analysis and neotype selection as given here, the genus *Collinsonia* (Labiatae) is considered to consist of only three species: *C. canadensis* L. (= *C. praecox* Walt., *C. tuberosa* Michx.); *C. serotina* Walt. (= *C. anisata* Sims, *C. punctata* Ell.); and *C. verticillata* Baldw. ex Ell. Recognition of infraspecific taxa within *C. canadensis* and *C. serotina* remains unresolved. In the belief, supported by the present evidence, that the mint named *Collinsonia serotina* by Thomas Walter (1788) is not distinguishable at the level of species from the plants later named *C. anisata* Sims and *C. punctata* Ell. — and secured by a typification that establishes its form as such — Walter's disregarded name regains its significance as a member of the Southeastern flora.

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TWO NEW SUBSPECIES OF *GILIA OCHROLEUCA* (*GILIA* SECT. *ARACHNION*: POLEMONIACEAE) FROM SOUTHWEST-CENTRAL CALIFORNIA

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ABSTRACT

One new subspecies is described, and one previously unrecognized taxon is recombined as a subspecies within *Gilia ochroleuca* M.E. Jones. **Gilia ochroleuca** subsp. **lanosa** Hrusa, **subsp. nov.**, occurs in sandy habitats within the San Rafael, Sierra Madre, and Topa Topa Mountains in the western Transverse Ranges of Santa Barbara and Ventura cos., California. It is a long-styled, rosette-forming annual, distinguished within the *Gilia ochroleuca* complex by its combination of lanate stem vestiture, monocaulic habit, and slender elongated cauline leaves with 1–2 short lobes generally at the base. **Gilia ochroleuca** subsp. **minima** (Eastw.) Hrusa, **comb. et stat. nov.**, based on *Gilia pedunculata* var. *minima* Eastw., occurs in the South Coast Ranges from central Monterey Co. to northernmost Santa Barbara Co. It is a small flowered, short-styled annual that has been mistaken for both *G. ochroleuca* subsp. *ochroleuca* and *G. minor*. Its similarity to *G. ochroleuca* subsp. *ochroleuca* appears due to parallel adaptation for self-fertilization. It bears only sectional relationship to *G. minor* and generic relationship to *G. pedunculata* Eastw. (= *G. achilleifolia* var. *multicaulis*). An emended description is provided, as the protologue described only how var. *minima* differed from *G. pedunculata*.

Verne and Alva Grant once stated that *Gilia* sect. *Arachnion*, the "cobwebby *Gilias*", "comprises the taxonomically most complex and critical group in the genus [*Gilia*] and perhaps in the entire family Polemoniaceae" (A.&V. Grant 1956). It is thus perhaps not surprising that in sect. *Arachnion* continuing studies in both field and herbarium have now revealed previously unrecognized entities. The Grants performed complex biosystematic work including intra- and interspecific crosses and hybrid meiotic analyses (V.&A. Grant 1960), in addition to morphological study. Their classification, modified slightly over the years, proposed five major morphological units with 18 species and 37 total taxa within sect. *Arachnion*. These five units were each given the informal rank of 'Group' (equivalent to subsection) and were identified by one of the members; thus the *Gilia ochroleuca* Group comprises the diploid taxa *Gilia ochroleuca*, its four subspecies, and *Gilia cana* with its five subspecies. The *Gilia tenuiflora* Group is the most diverse and largest. It comprises eight diploid and four allotetraploid species. Among the diverse diploid species are *Gilia leptantha* with five subspecies and *Gilia tenuiflora* with four. The *Gilia tenuiflora* Group also includes the tetraploid *Gilia opthalmoides* with its three subspecies; it is the only tetraploid species with significant intraspecific structure. Finally, the *Gilia latiflora* Group comprises two diploid species, *Gilia latiflora* with six subspecies and the monotypic *Gilia diegensis*.

Experimental crosses made within the species Groups indicated that the taxa treated as subspecies were variably interfertile (V.&A. Grant 1960) with several layers of isolating mechanisms; some did not form capsules, others did not set filled seed, others only filled few seeds, in others the filled seeds did not germinate, and in still others filled seeds produced vigorous and sometimes fertile hybrids. Meiotic irregularities in the less fertile hybrid offspring were frequent and occurred in

crosses both between Groups and within Group, in *Gilia ochroleuca* subsp. *exilis* there was structural divergence between at least two populations of that subspecies. Overall, the form of the irregularities indicated both translocations and inversions were contributing to the intersterility (V.&A. Grant 1960).

Morphologically the variation among and within these Groups is also complex. Specific assignment without complete material and a relatively well-stocked and curated herbarium can be frustrating, at worst it becomes a guess. The sources of the variability, according to the hypotheses formulated by the Grant's work (A.&V. Grant 1956), largely was interspecific and inter-subspecific hybridization, occurring both within and between Groups and combined with a degree of phenotypic plasticity.

Gilia ochroleuca subsp. lanosa

On a collecting trip into western Santa Barbara Co. in 1906, Alice Eastwood collected a *Gilia* somewhere between Zaca Lake and the Sisquoc River canyon. This specimen did not receive a preliminary identification nor was it identified over the next 109 years. More collections of that *Gilia* did not arrive at the California Academy of Sciences until 1957, well after Miss Eastwood's time at the Academy had ended. Although plants referable to subsp. *lanosa* were also found in 1929 by Ralph Hoffmann near Madulce Peak in eastern Santa Barbara Co., that specimen remained unidentified at the Santa Barbara Natural History Museum herbarium (SBM, now at SBBG). Two collections from the Sespe Gorge of Ventura Co. in 1934 and 1935, deposited at POM, were likewise not identified, and were the last collections until the 1957 specimen appeared at CAS. Intensive collecting in the region by Clare Hardham, Clifton Smith, Jim Blakely and their colleagues in the late 1950s and 1960s in the same general region increased significantly the number of collections and the known range (Fig. 1). Most were identified as *Gilia ochroleuca* subsp. *bizonata* or were left unnamed. This *Gilia* first came to the author's attention in 2005 when he collected it during field work documenting the flora of the Sierra Madre Mountains of Santa Barbara Co.

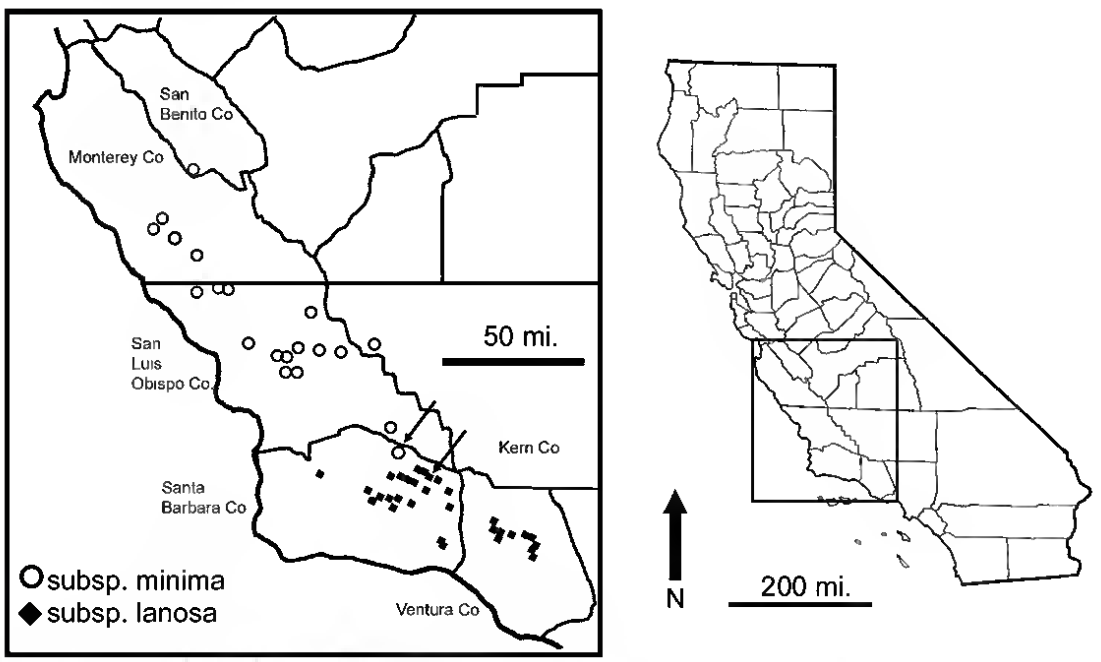

Figure 1. Known distribution of *Gilia ochroleuca* subsp. *minima* and subsp. *lanosa* in southwest-central California. Arrows indicate the type localities.

GILIA OCHROLEUCA M.E. Jones **subsp. LANOSA** Hrusa, **subsp. nov.** (Figs. 1, 2, 3A, 4, 5A-C). **TYPE: USA. California**. Santa Barbara Co.: Los Padres National Forest, Sierra Madre Mountains, white colored sandstone outcrop at head of Sweetwater Canyon, immediately S of Salisbury Potrero and E of Pine Corral Potrero, at base of slope on S side of Sierra Madre Rd., 34°48'48.87" N, 119°42'01.17" W, 4773 ft (1459 m), 20 May 2010, *G.F. Hrusa 18217 & M. Beyers* (holotype: CDA; isotypes: RSA, UC, DAV, CAS, OBI, SBBG).

Annuals, plants erect, 5–50 cm tall, gen. narrow, single stemmed (unless damaged), or with poorly to moderately developed secondary branches arising from above, or sometimes near, the rosette, but most frequently without significant secondary branching below the inflorescence. **Herbage** gray to grayish green. **Leaves** of the rosette fresh or dried at flowering, numerous or few, densely or thinly cobwebby pubescent on both surfaces, petiole narrower than the blade rachis, the blade pinnately lobed or weakly bipinnate with the pinnae short-lobed near the base or shallowly bifurcate at summit, the rachis narrower to rarely broader than the length of the lobes, 1–2 mm wide when fresh, the divisions narrower than the rachis or most often about the same width, sharp-tipped. Lowermost cauline leaves pinnate, the pinnae gen. in the upper 2/3 of the leaf. Middle cauline leaves sessile, linear, ascending to appressed, densely cobwebby, 8 to 25 mm in length, terminal lobe elongated, lateral lobes reduced, short triangular and near the lf. base, <1/6 as long as the leaf blade, in exceptionally vigorous plants sometimes with a second lobe near the base or near the tip, rarely longer than the width of the leaf rachis, or the leaves simple. Upper cauline leaves shorter than middle and lower cauline, generally like the middle cauline but more frequently simple. **Flowering stems** densely cobwebby, non-glandular pubescent below the first inflorescence branches, becoming less so at maturity. **Inflorescence** divaricately branched, at maturity frequently broader than tall, the branches not cobwebby, densely glandular to thinly glandular or rarely glabrous, and with a short, densely glandular section 1–3 mm long immediately below the calyx. **Bracts** glandular, cobwebby, or both, these 2–5 mm, simple or with a <1 mm pair of lobes near the base. **Bractlets** gen. simple 2 mm to <1 mm long, rarely with a pair of small basal lobes. **Flowers** 1–2 above a bractlet; the pedicels unequal, variable in length, 3 to 20 mm long, the longest 1.5 to 6 times longer than the shortest. Uppermost longer pedicel frequently with a 1.0–1.5 mm, simple bractlet in the lower half. **Calyx** 2 to 4 mm, glabrous or if thinly cobwebby when young, becoming glabrous at maturity, frequently purple or purple-streaked, blotched or spotted. **Corolla** 7 to 12 mm long, tube equal to or slightly longer than throat, gen. exerted from calyx <1mm, white, yellow, streaked purplish or purple in the upper part, thinly glandular in the upper part or glabrous, throat gradually expanded above the tube, yellow or pale in the lower half with blue-purple markings above, the lobes pink to purple-blue, 1.8–2.3 mm Stigma at maturity barely beyond, or up to 1.5 mm beyond the anthers, its branches 0.8–1.2 mm Stamens shorter than the corolla lobes, inserted immediately below the sinus, filaments ca. equal, 0.3–1.0 mm in length. Anthers 0.3–0.5 mm, equal, pollen blue. **Capsule** ovoid, at maturity 3 to 5 mm in length, as long as, or longer than the calyx lobes by up to ¼ its length. **Seeds** 1–4 per locule, 1.4 to 2.4 mm long and 0.7–1.2 mm wide, the color reddish to yellowish brown, with vermiculate ridges.

Additional specimens examined. **California**. Santa Barbara Co.: San Rafael Mountains, trail to Manzana Creek from Zaca Lake forest reserve, 22 Jun 1906, *Eastwood 667* (CAS); sandy flat, Madulce Ranger Station, 8 Jul 1929, *Hoffmann* (SBBG); 8 mi N of Manzana [Nira] Camp Ground, 29 May 1959, *Hardham 4688* (RSA); Manzana River at Fish Creek on trail to Hurricane Deck, 20 May 1957, *Hardham 2024* (CAS, RSA, SBBG); Pine Corral Potrero, roadbank in loamy soil, 23 May 1957, *Smith 5453* (RSA, SBBG); Hurricane Deck, 23 May 1960, *Hardham 5890* (CAS, SBBG, RSA); Santa Ynez River valley, Mono debris dam at confluence of Indian and Mono Creeks, 6 May 1962, *Breedlove 2679* (CAS, UCR, RSA); Sierra Madre Mountains, Montgomery Potrero, 11 May 1962, *Chandler 724* (RSA, SBBG); Fish Creek on Manzana [River], 23 May 1962, *Hardham 10224* (CAS, RSA, SBBG); Santa Ynez Mountains, bank of fire road near mouth of Indian Creek, upper Santa

Ynez River, 23 May 1962, *Smith 6871* (SBBG); Santa Ynez Mountains, bank of fire road near mouth of Indian Creek, upper Santa Ynez River, 23 May 1962, *Smith 6868* (SBBG); E end, Hurricane Deck, 24 May 1962, *Hardham 10225* (RSA); Sierra Madre Mountains, sandy flood plain, Sisquoc River at Tepusquet Rd. crossing, 24 May 1967, *Chandler 3400-A* (SBBG); sandy, rocky area along road, E of Pine Corral Potrero, 14 May 1973, *Smith 10565* (RSA, SBBG); Pine Corral Potrero, sandy bench, incised creek canyon below Cherry Orchard and James Springs at SE edge of potrero, 34°49'12" N, 119°43'16" W, 4480 ft, 4 Jun 2005, *Hrusa & Ragan 16594* (CDA, CAS); alluvium, open spots above Manzana Creek, ca. 3 mi downstream of Nira camp, W ca. ¼ mile of Coldwater Camp, 34°47'41" N, 119°58'46" W, 1800 ft, 10 Jun 2006, *Hrusa & Dougherty 16850* (CDA); Sierra Madre Mountains, white-colored sandstone outcrop at head of Sweetwater Canyon, immediately S of Salisbury Potrero and E of Pine Corral Potrero, 34°48'48.87" N, 119°42'01.17" W, 4773 ft, 30 Apr 2008, *Hrusa 17329* (CDA, RSA, DAV, CAS); Santa Barbara Canyon at Big Pine Rd., 6 May 2008, *Gross 3345* (RSA); Manzana Creek, ca. 0.7 km E of Lost Valley, ca. 1.3 km WNW mouth Fish Creek, San Rafael Wilderness, 600 m, 34.7655° N, 119.9149° W, 7 May 2008, *Wilken & Muller 16768* (SBBG); sandy upper alluvium, Sisquoc River ca. 3/4 mi. downstream from Sycamore Camp, 34°48'39" N, 119°49'07" W, 2100 ft, 29 Apr. 2008, *Hrusa 17212a* (CAS); Sisquoc River Canyon, open gravelly slope on disintegrating conglomerate, steep N slope of pinnacle on S side of river, W of Mine Canyon confluence, ca. ¼ mile E of Cliff Camp, 34°48'57" N, 119°50'46" W, 1970 ft, 9 May 2009, *Hrusa 17817* (CDA, CAS, UC); sandy floodwash zone among shrubs, Sisquoc River Canyon between Big Bend Canyon and Mine Canyon, 34°48'57" N, 119°50'01" W, 1870 ft, 9 Jun 2011, *Hrusa & Beyers 18384* (UC); uncommon on slope below Sierra Madre Rd. between Salisbury Potrero gate and Pine Corral Potrero, 34°48'59" N, 119°42'33" W, 4870 ft, 30 Apr. 2008, *Hrusa 17313* (CDA); Sisquoc River Canyon, ca. 2 mi E of Cliff Camp, 34°48'54" N, 119°49'59" W, 1855 ft, 9 May 2009, *Hrusa 17787* (CDA, CAS, UC, RSA); Sisquoc River, sandy and rocky fresh riverwash, first river crossing upstream from Sycamore Camp, 34°48'19" N, 119°48'26" W, 2010 ft, 10 May 2009, *Hrusa 17836* (CDA, UC, RSA, CAS, SBBG); sandy hillside, behind S wall of sandstone 'amphitheatre', Sweetwater Trail, ca. 4 mi. S of Sierra Madre Rd. on ridge between Sweetwater Canyon and Forester's Leap Canyon, 34°47'50" N, 119°44'43" W, 4505 ft, 13 Jun 2009, *Hrusa 17923* (DAV, SBBG); Ventura Co.: Topa Topa Mountains, sandy soil near Wheeler's Hot Springs, 1500 ft, 1 May 1934, *Munz 13206* (RSA); Brushy Flat, Sespe Creek, 900 m, 2 May 1935, *Clokey & Anderson 6821* (RSA, SBBG); Howard Creek, Sespe, 8 May 1961, *Hardham 6955* (RSA); shale hills opposite the Sandstone Camp, Rte. 399 [Hwy 33], 4500 ft, 8 May 1961, *Hardham 6962* (CAS, RSA, SBBG); shale hills opposite the Sandstone Camp, Rte. 399 [Hwy 33], 4500 ft, 8 May 1961, *Hardham 6963* (RSA); sandy soil, upper Sespe, Rte 399 [Hwy 33], 4500 ft, 16 Jun 1962, *Hardham 10339* (CAS, RSA [as 10399], SBBG); mouth of Derrydale Creek and Sespe River, 5 Jun 1963, *Blakley 5993* (RSA, SBBG); flat on Sespe Creek Rd. between Lion and Bear Canyons, 3000 ft, 1 Jun 1966, *Pollard* (CAS); Rte. 33 near Sandstone Camp, upper Sespe watershed, 4500 ft, 2 Jun 1967, *Chandler 3485-C* (SBBG); Hwy 33 at Sandstone Campground, upper Sespe Creek watershed, 2 Jun 1967, *Smith 9676* (SBBG); sandy flat near jtn. of Cherry Creek and Sespe Creek, upper Sespe watershed, 4000 ft, 21 Jun 1967, *Chandler 3583* (SBBG); upper Cherry Creek Canyon off Hwy 399 [Hwy 33], upper Sespe Creek watershed, 21 Jun 1967, *Smith 9835* (CAS, SBBG); Chorro Grande Cyn., draining into Sespe Creek from N off Pine Mountain, near US gypsum quarry, 7 Jun 1971, *Clarke PLM-2* (RSA).

The Gilia ochroleuca Group

Gilia ochroleuca subsp. *ochroleuca*, subsp. *exilis* (Gray) Grant & Grant, subsp. *bizonata* Grant & Grant, and subsp. *vivida* (Grant & Grant) Grant & Grant (Porter 2012) are regionally widespread taxa. *Gilia ochroleuca* subsp. *ochroleuca* occupies the California Mojave Desert margins; *G. ochroleuca* subsp. *bizonata* is frequent in the Transverse ranges from its northwestern limit near Mt. Pinos in Kern and Ventura Cos. to the San Gabriel Mtns. of Los Angeles Co.; *G. ochroleuca* subsp. *exilis* is centered south of Los Angeles Co., where it is most frequent in western Riverside and San Diego Cos.; and subspecies *vivida* has perhaps the smallest range among these four taxa, being

Figure 2. A Conditions at type locality of *Gilia ochroleuca* subsp. *lanosa*. The plants occur on the light-colored sandstone in wet years, on the margins of it in less well-watered years. The burned trees are 10–15 ft. tall *Pinus monophylla*. The type locality and much of the range of the subspecies in the Sierra Madre was burned in the 2009 La Brea fire, without obvious affects on the populations. B Plant material and edaphic conditions on the poorly consolidated white sandstone at the type locality. Note the single flowering stem with branching only above the base, the broad basal leaf rachises, and prominent elongated cauline leaves.

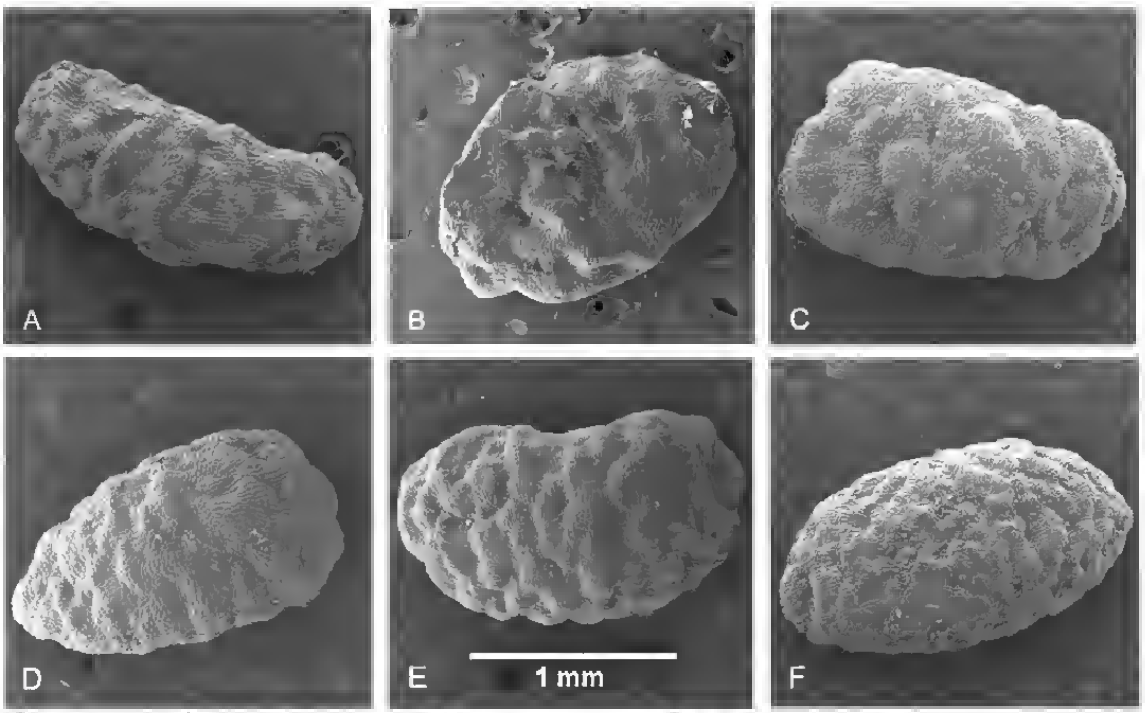

Figure 3. SEM micrographs of seeds of *Gilia ochroleuca* subspecies. A subsp. *lanosa* (*Hrusa 16594*, CAS), B subsp. *minima* (*Hoover 7084*, CAS), C subsp. *ochroleuca* (*E C. Twisselmann 8441*, CAS), D subsp. *bizonata* (*C B. Wolf 2438*, CAS), E subsp. *exilis* (*M E. Jones 6-20-1926*, CAS), F subsp. *vivida* (*J T. Howell 23405*, CAS). All images are scaled identically.

Figure 4. Type specimen of *Gilia ochroleuca* subsp. *lanosa* (*Hrusa 18217*, CDA). The single flowering stem with branching only above the base and the cauline leaves with elongated terminal and reduced lateral lobes are visible diagnostic features

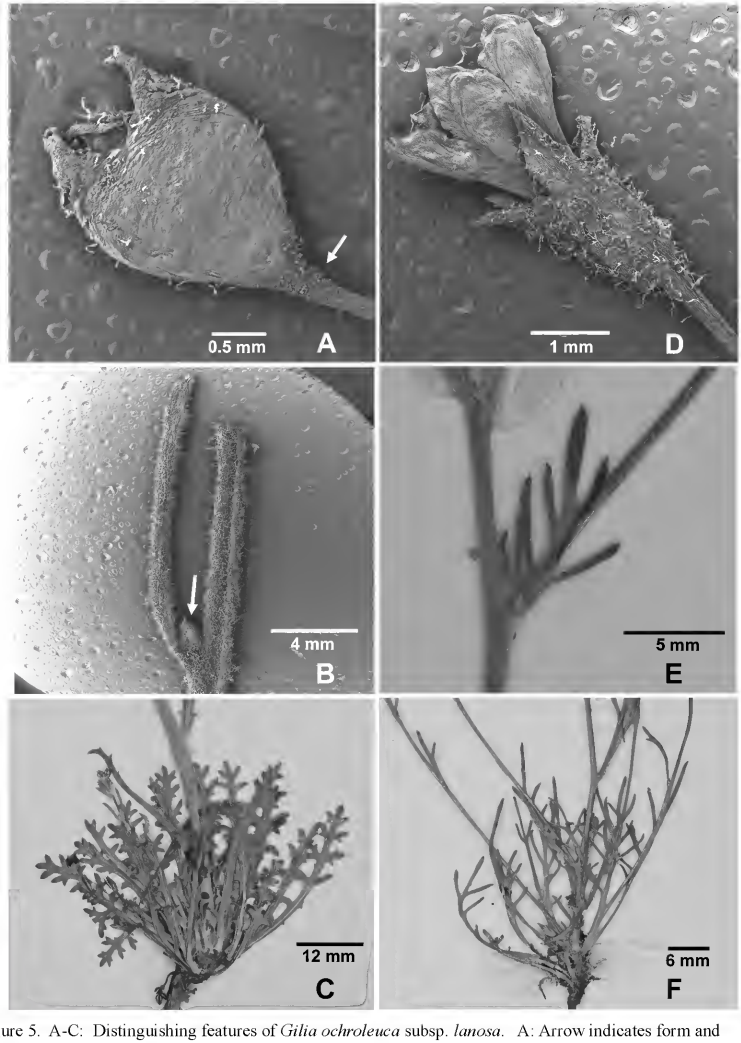

Figure 5. A-C: Distinguishing features of *Gilia ochroleuca* subsp. *lanosa*. A: Arrow indicates form and position of glandular ring at pedicel summit. B: Densely lanose cauline leaf and stem with elongated terminal lobe (also Figs. 2B, 4). Arrow indicates short lateral lobe. C: Basal leaf rosette with pinnate to weakly bipinnate leaves with broad rachis. D-F: Features of *Gilia ochroleuca* subsp. *minima*. D: Cobwebby calyx, with fully formed corolla. E: Comparative cauline leaf, typical of all subsp. of *G. ochroleuca* except subspp. *lanosa* and *vivida*. F: Basal leaf rosette, with slender, pinnate lobing.

restricted mostly to the San Gabriel Mtns. of eastern Los Angeles Co. It is perhaps important that the original formulation of the *Gilia ochroleuca* Group did not include subsp. *vivida* (Grant & Grant 1956). That taxon was originally proposed as a subspecies of *G. leptantha* in the *Gilia tenuiflora* Group and was later (V.&A. Grant 1960) transferred to the *G. ochroleuca* Group to indicate its relative interfertility with the tested members of the latter. It was anomalous in the *Gilia tenuiflora* Group, and while somewhat less so in the *Gilia ochroleuca* Group, within *G. ochroleuca* itself it is still the most distinctive among its subspecies. The taxon here proposed as *G. ochroleuca* subsp. *lanosa* is about as distinctive and may be the result of some of the same evolutionary processes elucidated experimentally for subsp. *vivida*, but which for subsp. *lanosa* can at this point only be inferred.

Within sect. *Arachnion*, the *Gilia ochroleuca* complex is distinguished by the combination of stamens inserted evenly on the corolla throat below the sinuses; a non-glandular calyx; a corolla tube as long as the throat or shorter, and barely exerted, the tube pale blue, blue purple, yellow or white, dilated sharply into the throat; the throat white or yellow at base, blue or purple distally, with a capsule at maturity that does not or barely exceeds the calyx. Even though considerable variation exists among the *G. ochroleuca* subspecies, subsp. *lanosa* is readily distinguished from the five named taxa in the complex (including subsp. *minima* described below) by the following: (1) terminal lobe of cauline leaves elongated, with 1–2 pairs of short, triangular leaf lobes generally at the leaf base, these in length not or barely exceeding the rachis width (Fig. 5B), vs. cauline leaves with several pinnate divisions, gen. at least 3–5x longer than the rachis width (Fig. 5E); (2) a persistent dense lanate tomentum on the stems and cauline leaves below the inflorescence (Figs. 4, 5B), vs. a less dense tomentum that disappears as the plant matures persisting only on the cauline leaves, or the stems glabrous; (3) glandular or mixed glandular and lanate bractlets, vs. bractlets glabrous or lanate only; (4) a single flowering stem per rosette with any branching only above the stem base (Figs. 2B, 4), vs. plants with multiple stems from the rosette (rarely otherwise); (5) a 1–3 mm dense patch of glands on the pedicel immediately below the calyx (Fig. 5A), vs. absent among the remaining taxa or in similar form of inconsistent occurrence in subsp. *exilis*; and (6) relatively elongated seeds, the length generally at least 2 times the width. Figure 3 displays mature, well-developed seeds of subsp. *lanosa* in comparison to those of the other *G. ochroleuca* subspecies.

Alva Day annotated one herbarium sheet as *Gilia ochroleuca* subsp. *bizonata* "variant with narrow corolla throat and small lobes." A small survey of lobe length against corolla length between subspp. *lanosa* and *bizonata* revealed no significant differences. The abrupt transition from tube to throat that distinguishes *G. ochroleuca* as a whole is indeed generally less markedly developed in subsp. *lanosa*, but among and within individuals there is considerable variation in the feature and it is not reliably diagnostic. Subspecies *lanosa* is readily distinguished from subsp. *bizonata* by its dense lanate tomentum, glandular inflorescence, broad basal leaf rachis and divisions, and single flowering stem. Subspecies *bizonata* is mostly glabrous, has narrow leaf divisions, and almost always has several or many stems originating at the rosette. The only seeming morphological similarity of subsp. *lanosa* to any other *ochroleuca* variant, beyond the typical stamen and corolla configuration, is with subsp. *exilis*; both taxa may have a dense 1–3 mm wide patch of glandular trichomes at the pedicel summit (Fig. 5A), a feature absent in subspp. *bizonata*, *minima*, and *ochroleuca* but which does appear in several other taxa of sect. *Arachnion*. In subsp. *exilis* the similar glandular ring is inconsistently present and when present is less dense and less sharply delimited than it is in subsp. *lanosa*. Likewise if the glands on the inflorescence rachis in subsp. *vivida* are particularly dense below the calyx they may at times also resemble the glandular ring in *lanosa* or *exilis*. In the opinion of this author these features are not directly homologous. However, their glandular rings may share a similar derivation via interspecific gene flow. Subspecies *lanosa*, *vivida*, and *exilis* otherwise share few features. Compared to subsp. *lanosa*, subsp. *exilis* is especially variable as to basal leaf divisions: these may be weakly bipinnate, pinnate, or simple, but the divisions, when present, are always slender

and generally more than 5 times longer than the rachis width, similar to those of subspecies *minima* (Fig. 5F). The basal leaves of subspecies *lanosa* are pinnate or shallowly bipinnate, with the rachis and lateral divisions broader than in subsp. *exilis* and from less than 1 to (rarely) 4–5 times as long as the primary rachis width (Figs. 2B, 4, 5C). In vigorous specimens, the broad leaf rachis of subsp. *lanosa* is somewhat similar to that of subspecies *vivida* although never tripinnate. Overall, subsp. *lanosa* can be distinguished from subsp. *vivida* by (1) its upright simple stem vs. multiple stems spreading from the base; (2) its non pungent rosette leaves that are never more than bipinnately compound, vs. pungent tipped leaf divisions with leaves up to tripinnately compound; (3) basal leaf tomentum predominantly on the adaxium, vs. the leaf tomentum concentrated on the abaxial surface in subsp. *vivida*; and (4) its elongated and overall longer cauline leaves without pungent tips, contrasts with the shorter and pungently tipped leaves of subsp. *vivida*. It is separable from subspecies *ochroleuca*, *exilis*, *minima*, and *bizonata* by its rosette leaf divisions with broad rachis. A single unusual specimen of subsp. *exilis* from Riverside Co. (*Peirson 921*, CAS, RSA) had a single terminal flowering stem and reduced cauline leaf lobes. It could be distinguished from *lanosa* by its slender, simple basal leaves and non-lanate stems.

Alva and Verne Grant (1956, 1960) suggested the hypothesis and supported it with experimental data — that the exceptionally broad and tomentose rosette leaves of subsp. *vivida* were derived via gene flow from somewhere in the *Gilia cana* and/or *Gilia leptantha* complexes (members of the *Gilia ochroleuca* and *Gilia tenuiflora* Groups, respectively). Indeed, the basal rosette of subsp. *vivida* can be matched by those of several subspecies of *G. cana*. The basal rosette of subsp. *lanosa* is less divided and less tomentose than that in subsp. *vivida*; it bears considerable resemblance to those in the *Gilia leptantha* complex (*Gilia tenuiflora* Group) and in some individuals to those in the *Gilia latiflora* Group, which are generally simply pinnate with a broad rachis. Morover, the ring of glandular hairs below the calyx is an occasional feature of taxa in both the *Gilia cana* and *Gilia latiflora* complexes. It is possible that at least some of the distinctive variation in subsp. *lanosa* is the result of gene flow from *G. cana*, *G. leptantha*, *G. latiflora*, or some other current or extinct taxon of sect. *Arachnion*. The form of the cauline leaves in subsp. *lanosa*, with their reduced lateral lobes and elongated central lobe is not known, however, in any other member of the section and suggests the possiblity that its cauline leaf form has developed independently. One is struck by the similarity of shape between these cauline leaves and the shape of the uppermost floral bracts throughout sect. *Arachnion*. A hypothesis of the elaboration of previously reduced floral bracts to become the cauline leaves of subsp. *lanosa* is, at present, purely conjectural.

Gilia ochroleuca subsp. *lanosa* is restricted to the San Rafael, Sierra Madre and Topa Topa Mtns. in Santa Barbara and Ventura cos. (Fig. 1). It is most common about the south sides of the potreros and associated sandy ridges along the south face of the summit of the eastern Sierra Madre (Fig. 5A); it is also found on the sandy floodplain of the middle reaches of the Sisquoc River that drains the south face of the Sierra Madre. Indeed it was probably along the Sisquoc River floodplain that Miss Eastwood discovered the plant. It is less common in the next parallel drainage to the south, (the Santa Ynez River) but is frequent in the Sespe River Gorge of the Topa Topa Mountains about 25 miles east in Ventura Co. Its primary habitat is on relatively sterile, sandy soils (rarely on gravel), within oak woodlands, chaparral, and openings in pinyon pine (*Pinus monophylla*) forest (Fig. 2A). The majority of the known populations occur within the San Rafael Wilderness, a roadless watershed preserve covering the headwaters of the Sisquoc River and Manzana Creek. Wilderness designation includes the south face of the Sierra Madre and north face of the San Rafael Mountains.

As frequently seen in annual plants, subsp. *lanosa* growing under stress or other dwarfing conditions responds by not only reducing the size of the plant body but by simplifying its complexity. Stressed dwarfs often have rosette leaves with few or no divisions, have few hairs of any kind, may lack the distinctive glandular ring below the calyx (Fig. 5A), and have few rosette leaves. These

specimens can be extremely difficult to identify with certainty. Clearly, plastic responses in this taxon are as frequent as expected in an annual plant growing only during the variably moist California spring season.

From a conservation standpoint, in spite its limited distribution *Gilia ochroleuca* subsp. *lanosa* is quite secure. Its range is mostly within an established National Wilderness area. Some of the populations are large and there are no threats to any of those in the part of the Sierra Madre Mts. that does not have wilderness status. Those in the Topa Topa Mts. may not be as secure but at present, aside from their existence on and near a State Highway roadside, there appear not to be any immediate threats.

Subspecies *lanosa* is named for the dense lanose indument on the stems up to the first inflorescence branches, especially dense in the early season. The density and coverage of this indument distinguishes it from all other subspp. of *Gilia ochroleuca* and suggest possible gene flow from contact with plants referable to the generally tomentose *Gilia cana* complex. The lanate indument generally thins as the plant ages, and older, fruiting specimens may show this characteristic feature only on the lowermost stem and/or only on the middle cauline leaves and in that feature appear like subsp. *exilis* or subsp. *vivida*. The indument is most visible in Fig. 5B and on the type specimen (Fig. 4).

In the protologue to *Gilia pedunculata* var. *minima*, Eastwood cited the *G. pedunculata* var. *pedunculata* description, which is that of a different taxon (now *G. achilleifolia* subsp. *multicaulis*), with comments to accomodate the perceived form of var. *minima*. For that reason an emended description of *G. pedunculata* var. *minima* is provided here.

GILIA OCHROLEUCA M.E. Jones subsp. **MINIMA** (Eastw.) Hrusa, **comb. et stat. nov.** (Figs. 3B, 6). *Gilia pedunculata* Eastw. var. *minima* Eastw., Bot. Gaz. 37: 447. 1904. *Gilia pedunculatis* Eastw. ex Milliken var. *minima* (Eastw.) Brand, Pflanzenreich, Heft 27: 108. 1907. **TYPE: USA. California.** Santa Barbara Co.: Cuyama, 7 May 1896, *A. Eastwood s.n.* (holotype: CAS 00123859, high res. digital image!). An isotype specimen at B (cited by Brand 1907) may not have survived World War II. Not *Gilia minima* (Nutt.) Gray, Proc. Amer. Acad. Sci. 8: 268. 1870 (based on *Navarretia minima* Nutt.).

Annual, erect, 5–25 cm. tall, upright, slender, single or more frequently multi-stemmed. **Stems** non-glandular, cobwebby pubescent below and at the nodes, occasionally the stems thinly cobwebby, otherwise mostly glabrous. **Basal leaves** in a sparse rosette, pinnate, glabrous or the adaxium cobwebby pubescent near the base, the lobes linear, two to six or more on each side, gen. not paired, the lobes becoming slightly broader towards the obtuse tip, 5–10x or more longer than the width of the rachis. **Cauline leaves** pinnate, sessile, 8 to 15+ mm in length, the pinnae of 2–4 linear lobes from near the leaf base, these ½ or more as long as the leaf blade, 8–10 times in length the width of the rachis, glabrous or most often cobwebby in the lower parts, obtuse at the lobe tips, not pungent. **Inflorescences** divaricately branched, cobwebby at the nodes, thinly glandular to glabrous above, rarely cobwebby; when the rachis glandular it is without a ring of glands at the pedicel summit. **Bracts** with a single pair of lobes near the base, these shorter to as long as the bract, cobwebby pubescent to glabrate, the hairs gen. restricted to the base of the leaf and the associated node. Upper bracts reduced and frequently simple above, 1.5–5 mm in length. **Flowers** 1–2(–3) above a nodal bractlet, pedicels unequal. **Calyx** 2.0 to 2.5 mm, densely to thinly cobwebby, often becoming less so in age, the ribs green or purple throughout or purple only in the lower half; the membrane smooth, not folded, purple spotted, streaked, or purple throughout, both the rib and membrane pigments frequently faded in aged herbarium specimens. **Corolla** 2 to 4 mm in length. Tube included in the calyx, equal to or slightly longer than the throat. The tube pale yellowish or white, the throat pale with a small yellow zone or spots near the summit (as per label data), the limb

pale or dark blue, frequently streaked, 1–1.5 mm in length. **Style** maturing among the anthers, the stigma lobes 0.2–0.3 mm long. **Stamens** inserted immediately below the sinus, shorter than the corolla limb, filaments equal, 0.1–0.2 mm **Anthers** 0.1–0.2 mm, equal, pollen blue. **Capsule** smooth, ovoid at maturity, 2.8 to 3.2 mm in length, as long as or shorter than the calyx lobes. **Seeds** 1–3 per locule, 1.2 to 1.6 mm long and 1.0–1.2 mm wide, orange-brown, transverse ridges few uneven.

Additional collections examined: **California**. Kern Co.: Summit of Messa Ridge [W of Carneros Rocks], Temblor Mountains, *Quercus douglasii* association, 3400 ft, 12 May 1955, *Twisselmann 1965* (CAS); Monterey Co.: Jolon, 4 Apr 1915, *Eastwood* (CAS); Santa Lucia Mountains, sandy soil, N slopes, *Quercus douglasii* assoc., hills along the San Antonio, Pleyto, [Pleyto submerged in San Antonio Reservoir, 1965], 28 Mar 1960, *Hardham 5258* (CAS504101, RSA140764; not *Hardham 5258* CAS871396, RSA555426); Santa Lucia Mountains, sandy N slope opposite Bee Rock (S side of road), 1000 ft, 28 Mar 1960, *Hardham 5258* (RSA555426, CAS871396; not *Hardham 5258* CAS504101, RSA140764); Santa Lucia Mountains, sandy bed of river ca. 2 mi N of San Antonio Mission, Sulphur Creek Canyon, 7 Apr 1960, *Hardham 5401a* (CAS, RSA); hills N of San Antonio Mission, 10 Apr 1960, *Hardham 5369* (RSA); same data, *Hardham 5469* (CAS, SBBG); San Benito Co.: San Lorenzo Creek near jtn. with San Benito River, 2000 ft, 1 May 1933, *Ferris 8367* (DS, RSA); San Luis Obispo Co.: El Dorado School, Santa Margarita, 11 May 1933, *Wall s.n.* (CAS); in coarse sand, Atascadero, 29 Mar 1947, *Hoover 6783* (UC); sandy flat, Yaro Creek district, N of Pozo, 10 Apr 1947, *Hoover 6992* (CAS, UC); on sandy flats, upper Toro Creek, N of Pozo, 26 Apr 1947, *Hoover 7084* (CAS, UC); Fernandez Creek, near N base of La Panza Range, 23 Mar 1947, *Hoover 6727* (CAS, UC); on sandy flat in area swept by fire last summer, Upper Navajo Creek, La Panza Range, 12 Apr 1947, *Hoover 6909* (CAS, UC); rd. between El Dorado School and Pozo at Yaro Creek bridge ca. 7 mi N of Pozo, 25 May 1955, *Ferris 12835* (DS); hills between San Juan River and Carissa Plains, Paso Robles-Simmler Rd, 28 Apr 1958, *Hardham 3132* (CAS, RSA, SBBG); Santa Lucia Mountains, low sandy depression in full sun, Cantinas Creek, 800 ft, 4 Apr 1960, *Hardham* 5299 (CAS, RSA, SBBG); Santa Lucia Mountains, N slope, Bee Rock, 28 Mar 1960, *Hardham 5250* (SBBG); bare sandy soil, *Pinus sabiniana* woods, intersection Cammatta Road and Shell Creek Road, 8 Apr 1960, *Hardham 5365* (CAS, RSA, SBBG); sandy bed of Huero Huero R. east branch, near Calf Canyon Rd. (S of Creston), 10 May 1963, *Hardham s.n.* (CAS); Bedell Ranch, 5 mi. SE of Creston, 1150 ft, 24 Apr 1969, *Twisselmann 15153* (CAS); California Dept. Fish & Game Ecological Reserve, N side Cuyama Valley on lower S face of Caliente Range, openings in *Atriplex canescens* scrub, on broad sandy ridge, 35°03'34.26" N, 119°54'35.25" W, 1915 ft, 3 Apr 2008, *DFG anon.* (DAV).

Examination of *Gilia* specimens from San Luis Obispo and Santa Barbara Cos. revealed that a diminutive form from the interior of the South Coast Ranges was clearly within the *Gilia ochroleuca* Group but occurred north of its reported range and with a distinctive morphology. Herbarium specimens were sometimes determined (and annotated) by Alva Day [Grant] as a "small-flowered form of *Gilia bizonata*," while others were annotated by Clare Hardham as a "self-pollinating form of *Gilia exilis*." They were mentioned by both Grant and Grant (1956, p. 224) and Hoover (1970, p. 227, under *Gilia minor*), neither of whom drew further taxonomic conclusions.

A further survey of existing *Gilia* types from central California found that the type of *Gilia pedunculata* Eastw. var. *minima* Eastw. represented this entity. Eastwood described the variety as "similar to the preceding [*G. pedunculata* = *G. achilleifolia* var. *multicaulis*] in every way, but flowers and fruits less than half as large, and whole plant smaller" (Eastwood 1904). However, the type specimen of var. *minima* is not at all like *G. pedunculata*. Rather than having single-flowered inflorescences on long peduncles, it has an open, multiflowered, divaricately branched inflorescence with spreading pedicellate flowers. Among the listed exsiccatae the four individuals on the type sheet

(Fig. 6) were among the most robust specimens seen of this subspecies. All but a few individuals on the herbarium sheets cited above are more slender, less branched, and of smaller stature than the type.

Figure 6 Type specimen of *Gilia pedunculata* subsp *minima* = *G. ochroleuca* subsp *minima* (*Eastwood s.n.*, CAS).

Gilia ochroleuca is readily separated from *G. pedunculata* (= *G. achilleifolia* var. *multicaulis*) by many features, the following most notable: pedicellate vs. essentially sessile flowers; divaricate, open, multiflowered inflorescences vs. capitate inflorescences with variable numbers of flowers per capitulum — including the occasional reduction to a single flowered inflorescence as in the *G. pedunculata* type; and leaves in a basal rosette, rapidly diminishing upwards into bracts versus in var. *multicaulis* the leaves not in a basal rosette, stems leafy, the leaves little reduced upwards.

Subspecies *minima* most resembles the small-flowered subsp. *ochroleuca* of the Mojave Desert, and the type specimen was so annotated by Alva Day in 1976 (Fig. 6). Another specimen, collected near "Pozo, San Luis Obispo Co." by R.S. Ferris (CAS) was annotated by Day as an undescribed taxon, "distinct from subsp. *ochroleuca*." Like the typical subspecies, *minima* is short-styled; the style and stigma do not extend beyond the anthers, and mature flowers usually have the stigmas coated with pollen grains. Subspecies *minima* is usually more gracile than subsp. *ochroleuca*, the leaf divisions have obtuse rather than acute tips, and subsp. *minima* more frequently has simple bracts, while in subsp. *ochroleuca* the inflorescence bracts are pinnate or subpalmate up to their distal limit. The mature seeds of subsp. *minima* are foreshortened in comparison to the remainder of *G. ochroleuca*, being usually only about 1.2–1.5 times as long as wide (Fig. 5B), while those of subsp. *ochroleuca* are about 2 times as long as wide (Fig. 5C; also Johnson et al. 2004). In subsp. *minima* the calyx may be thinly cobwebby or densely and persistently so with the tomentum thinning only at full fruit maturity (Fig. 5D); in subsp. *ochroleuca* the calyx is generally glabrous from the beginning, although immature calyces may have a few cobwebby hairs. The membrane between the calyx ribs of subsp. *minima* is wholly or in part purple in color, being solid, streaked, or colored only in the lower half; only rarely is it uncolored. In subsp. *ochroleuca* it is always uncolored (white). The inflorescence branches of subsp. *minima* are completely glabrous or have glands scattered thinly throughout, while in subsp. *ochroleuca* the inflorescence branches are more or less glandular only immediately above each node. Grant and Grant (1956) considered the apparent similarity of subsp. *minima* to *G. ochroleuca* subsp. *ochroleuca* to be a case of parallel evolution and interpreted subsp. *minima* as a "reduced form of *G. o.* [subsp.] *bizonata*." The degree of its relationship with subsp. *bizonata* is at present not understood but it differs from that subspecies in its smaller corollas, included style, persistently cobwebby calyx, foreshortened seeds, fewer basal rosette leaves, and obtuse-tipped leaf divisions.

In the spring of 1947, Robert F. Hoover collected subsp. *minima* five times in the La Panza Range of San Luis Obispo Co. He discussed these plants and ultimately interpreted them as *Gilia minor* V. & A. Grant (Hoover 1970). A mixed sheet (*Hardham 3132*, RSA) collected in the San Juan Hills west of the northern part of Carrizo Plain indicates that *G. minor* is at least occasionally sympatric with subsp. *minima*. *Gilia minor* is also present in the adjacent Caliente Mtns. and on the hilly margins of Carrizo Plain itself. Compared to subsp. *minima* it is similarly small-flowered, short-styled, and self-pollinated. It is well differentiated from subsp. *minima* by its glandular, non-cobwebby calyx, unequal stamens, shorter and more numerous basal and cauline leaf divisions, and mature capsule about twice as long as the calyx. In contrast, all forms of *G. ochroleuca* have a non-glandular calyx, equal-length stamens, and a capsule slightly shorter than to barely exceeding the fruiting calyx. Hoover (1970) listed these plants as distributed only east of the Salinas Valley in the region between Atascadero and Pozo. He did not cite the plants from west of the Salinas Valley collected by Hardham. Monterey County specimens of *G. ochroleuca* were listed by both Howitt and Howell (1964) and Matthews (1997) as subsp. *bizonata*. The specimen(s) cited by Howitt and Howell from "near San Antonio Mission" are subsp. *minima*, but the single known collection cited from the "Palisades of the Nacimiento River" (*Hardham 5772*, CAS, RSA) is a different, still uncharacterized entity within the *Gilia ochroleuca* complex. Only the Palisades location (as "Hunter-Liggett") was mentioned in Matthews (1997). Genuine subsp. *bizonata* does not occur in either San Luis Obispo or Monterey Cos. *Gilia clivorum* is also frequent in the same regions. It can resemble

subsp. *minima* but is easily distinguished by a dark spot in the corolla throat below each lobe, a lack of lanose tomentum and/or cobwebby hairs, and the absence of a distinct basal leaf rosette. It occurs on more fertile soils and in more shaded conditions than does subsp. *minima*.

According to label data, subsp. *minima* occupies gravelly or sandy openings within chaparral, open grasslands, or oak savannah. It frequently occurs among rock outcrops where the topsoil is thin, in dry sandy creekbeds, or in sandy "depressions" within chaparral. It appears to grow in sites that inhibit the competitive growth of associated annual grasses or other weedy taxa; noted associates include several poorly competitive short season annuals including *Mimuartia pusilla* and *Pentachaeta exilis*. It has been found from about the latitude of King City in Monterey Co. to the north side of the Cuyama Valley on the boundary of San Luis Obispo and Santa Barbara cos. (Fig. 1). An attempt to locate this taxon in spring 2014 was unsuccessful, likely due to the unusually dry winter of 2013/2014. Some of the listed associates were found in the habitats described, and it may be that subsp. *minima* needs at least a reasonably wet winter to appear in the following spring. Compared to the type specimen, all but a few individuals on the known herbarium sheets are diminutive and suggest that in most years in which it appears at all, the plant may not reach its full vigor and growth potential. Despite the lack of recent collections, subsp. *minima* does not appear to be a particularly rare plant, with the known occurrences spread widely throughout the inner South Coast Ranges (Fig. 1). A note to Alva Day Grant from Clare Hardham, currently in the pocket of *Hardham 5258* (CAS) dated 5-14-60, stated that the plant is "very common-almost as ubiquitous as *Gilia clivorum* … ". In addition to environmental factors that may limit the frequency with which it appears, at least two additional factors contribute to the lack of newer documentation: first, the plants slender stature and sparse foliage make it easily overlooked; and second, its entire known distribution is on private land to which access, since 1960, has become increasingly restricted.

Both subspecies *lanosa* and *minima* occupy the extreme northwestern edge of the *Gilia ochroleuca* complex's distribution. The (probably) outcrossing subsp. *lanosa* is the most narrowly distributed form within the complex, having so far been found only in a remote region of perhaps fifty square miles (Fig. 1). The habitats where it is found are not unlike those of subsp. *exilis* or *bizonata*. Subspecies *lanosa* is an isolated morphological form within *G. ochroleuca*. Its distinguishing features suggest contact and gene flow from other species, particularly those in the *Gilia cana*, *Gilia leptantha*, or *Gilia latiflora* complexes and as such may be a recent result of fluctuating climates in the post-Pleistocene. Its cauline leaves however, suggest an independent derivation of that feature, and subsp. *lanosa* may just as well be a relictual taxon (Lancaster & Kay 2013).

Conversely, the seldom seen subsp. *minima* occupies a wide geographic range, with a north to south distribution of more than 110 miles (Fig. 1). It occupies a low elevation region with an early, short growing season and appears to occupy habitats that are not highly competitive. Its fruits and seeds are on average the smallest and the seeds fewest per locule among the *Gilia ochroleuca* subspecies. To judge from its short-styled, apparently self-fertilizing reproductive system, and adaptation to a short growing season, it may be a recent addition to the increasingly xeric post-Pleistocene conditions of central California.

I offer the following modifications to the dichotomous key by Porter (2012) in The Jepson Manual to account for subspp. *lanosa* and *minima*.

31. Corolla throat yellow or white with five yellow spots at base ..... **Gilia clokeyi, G. opthalmoides**
31. Corolla throat yellow or pale proximally, blue or pale distally.

32. Corolla 4–7 mm; throat yellow-spotted, </= lobes; calyx lobes short-pointed .... **Gilia clokeyi**
32. Corolla 7–12 mm; throat yellow >/= lobes; calyx lobes acuminate ..... **Gilia opthalmoides**

33. Stems mostly glabrous below the inflorescence. Without dense ring of short glandular trichomes immed. below the calyx.

34. Basal leaf rachis and divisions narrow, 1 mm or less wide. Basal leaves thinly floccose or +/- glabrous. Lower branches +/- spreading.

35. Corolla 8–14 mm; style > stamens. Calyx glabrous at maturity ..... **Gilia ochroleuca** subsp. **bizonata**

35. Corolla 4–6 mm. Style gen. = stamens. Calyx glabrous or cobwebby.

36. Calyx gen. persistently cobwebby, sometimes shedding most of the tomentum in age. Calyx membranes gen. purple or purple-streaked. Stems slender, upright. South Coast Ranges ..... **Gilia ochroleuca** subsp. **minima**

36. Calyx gen. glabrous. Membranes white. Stems slender to stout, spreading or upright. Mojave Desert and margin ..... **Gilia ochroleuca** subsp. **ochroleuca**

34. Basal leaf rachis and divisions broader, 2–4 mm wide. Basal leaves generally densely cobwebby tomentose. Plant low, stems spreading ..... **Gilia ochroleuca** subsp. **vivida**

33. Stems densely to partially floccose below the first inflorescence branches. A +/- dense ring of short-stalked glands freq. present on pedicels immediately below the calyx.

37. Plant scapose, simple or branched weakly above the base, strictly upright. Basal leaves 1–2 pinnate with 2–3 mm wide divisions and rachis. Stems densely lanate, (less by late maturity); terminal lobe of cauline lf. elongated, lanate, lanceolate-linear, with 1–2 pairs of short deltate to lanceolate divisions near base, in length 1–3 times the rachis width ..... **Gilia ochroleuca** subsp. **lanosa**

37. Plant gen. with multiple branches from the base, the lower spreading. Basal leaves 0–2 pinnate with narrow, 1 mm wide divisions and rachis, or leaves simple. Stems cobwebby in the lowermost parts, the lower and middle cauline leaves thinly lanate or glabrous terminal lobe similar to the laterals, with 2–3 pairs of elongate linear divisions, their length 3–10 times the rachis width ..... **Gilia ochroleuca** subsp. **exilis**

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VARIATION IN *EVOLVULUS NUTTALLIANUS* (CONVOLVULACEAE) IN CENTRAL TEXAS

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ABSTRACT

The normally pubescent *Evolvulus nuttallianus* Schult. occurs with a purely glabrous form in northern Hays County, Texas. The origin of the glabrous form may be, in part, the result of its location at the eastern edge of this taxon. Both the glabrous and pubescent forms in northern Hays Co. share atypical ovate-lanceolate sepals, another feature known from the eastern edge of its range. A revised key for *Evolvulus* species in Texas is presented.

Strong pubescence has been noted as a key characteristic within the genus *Evolvulus* in Texas treatments, but especially for *E. nuttallianus* Schult. (syn. *E. pilosus* Nutt.). Common name epithets for this species include shaggy, silky, hairy, silver, and woolly. *Evolvulus nuttallianus* reaches the southeasternmost edge of its distribution in northern Hays County, Texas, near the eastern edge of the Edwards Plateau and west of the Balcones Escarpment (Map 1). *Evolvulus nuttallianus* is relatively rare in this area — the species is represented in TEX/LL herbaria by very few vouchers in this area: 5 in Travis County (most recent in 1950), 2 in Hays County (mine, 2003), 1 in Blanco County (1987), 1 in Bexar County (no date, no location). Recent sightings by Terri Siegenthaler and the author from western Travis County have been from the Shield Ranch and the Hamilton Pool Nature Preserve.

A population of ±20 small plants, at least half of them lacking hairs, is found in northern Hays County on the private Purola Preserve and an adjacent ranch, on a high barren ridgetop in a sunny calcareous sandy opening in oak-juniper association. All parts (i.e., leaves, stems, sepals) of the glabrous plants lack hairs, and although small (less than 5–12 cm tall), even from a distance of several yards their glossy appearance is eye-catching (Figs. 1–5). These grow in close association with the pubescent plants (Fig. 2), but no intermediate forms occur. First noted in the 1990s, the glabrous population has persisted, surviving the exceptional droughts of 2006 and 2008.

The hairs of the pubescent plants are essentially the same as those found on *Evolvulus nuttallianus* elsewhere in Texas, certainly not smaller, although less dense (Figs. 6-8, Map 2).

Associated taxa at the Purola Preserve include *Evolvulus sericeus*, *Polygala lindheimeri*, *Chamaesyce fendleri*, *Hedeoma reverchonii* var. *reverchonii*, *Stenaria nigricans* var. *nigricans*, and *Schizachyrium scoparium*. No other populations of *E. nuttallianus* are known from the immediate vicinity. Voucher specimens of individuals from this site are deposited at TEX (*Harms 43-A*, glabrous, Figs. 9–10; *Harms 43*, pubescent, Fig. 11).

One atypical feature of both *Evolvulus nuttallianus* forms in northern Hays Co. is their ovate-lanceolate outer sepals (Fig. 4). This is also noted from other collections from the eastern edge of its range (Map 1). This contrasts with the typical lanceolate to narrowly lanceolate sepals found elsewhere, although similar to the ovate sepals of closely related *E. arenarius* on the Texas/New Mexico border (Harms 2014).

Although the origin of this glabrous form is not known, several factors seem relevant. First, *Evolvulus nuttallianus* is at the eastern edge of its range and relatively rare in this area. No other populations are known from the immediate vicinity. Second, a west-to-east clinal reduction of hair density occurs in *E. nuttalliamus*, with the eastern populations (like this one) being the most sparsely pubescent (Map 2). Third, *E. sericeus*, with glabrous upper leaf surface and ovate sepals, occurs in the immediate vicinity of the glabrous population, and so the possibility of hybridization must be considered. Whether the glabrous form originated from a random single-gene mutation, hybridization, or chance allelic combinations, low population density and apparently relaxed selection for pubescence density probably are factors in its origin, persistence, or both.

Revised *Evolvulus* key for Texas

Current Texas keys rely heavily on pubescence, especially to distinguish *Evolvulus nuttallianus* and *E. sericeus*; e.g., Shinners (1970); Diggs et al. (1999). Sepal form, following van Ooststroom (1934), is also used; e.g., Diggs et al. (1999); Austin (1998). In so far as possible I have avoided these differentiae, especially distinctions of hair habit and density.

1. Leaves with palmatipinnate venation (generally visible on some leaves without clearing); upper leaf surface glabrous with lower leaf surface pubescent, or both surfaces pubescent; phyllotaxis distichous ..... **Evolvulus sericeus**
1. Leaves with pinnate venation; both leaf surfaces pubescent or both glabrous; phyllotaxis distichous or pentastichous.

   2. Phyllotaxis distichous; inflorescence with peduncles >6 mm and few-flowered cymes ..... **Evolvulus alsinoides**
   2. Phyllotaxis pentastichous 2/5; inflorescence with peduncles <6 mm (rarely >0.5 mm) and solitary flowers.

      3. Foliage sparse with internodes commonly >4 mm; mid leaves linear, length/width ratio >8:1; trichomes asymmetrical with short forks <0.25 mm long ..... **Evolvulus arenarius**
      3. Foliage dense with internodes rarely >4 mm; mid leaves elliptical, length/width ratio <8:1; trichomes asymmetrical with short forks >0.25 mm long ..... **Evolvulus nuttallianus**

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Figure 1. *Evolvulus nuttallianus* glabrous with emerging small plants 4 Jun 2014

Figure 2. Pubescent form on left, glabrous form on right. 2 May 2010.

Figure 3. Glabrous form detail (via dissecting microscope). 4 Jun 2014.

Figure 4. Ovate-lanceolate outer sepals; glabrous form on left.

Figure 5. Glabrous form leaf scans (top), venation with cleared leaf (bottom).

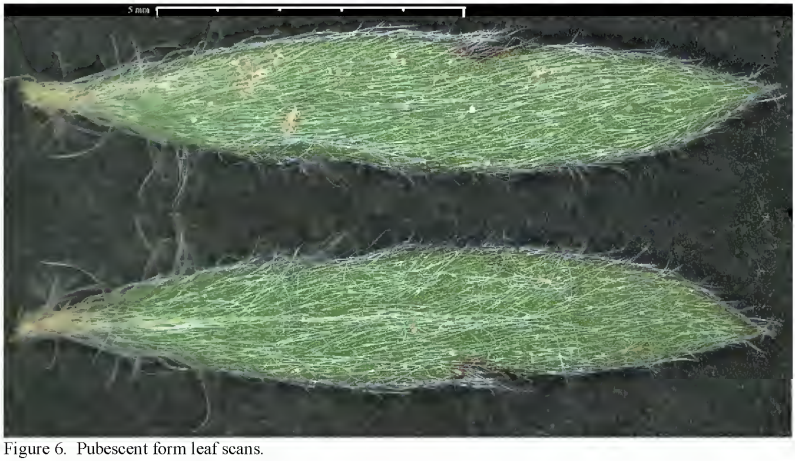


Figure 6. Pubescent form leaf scans.

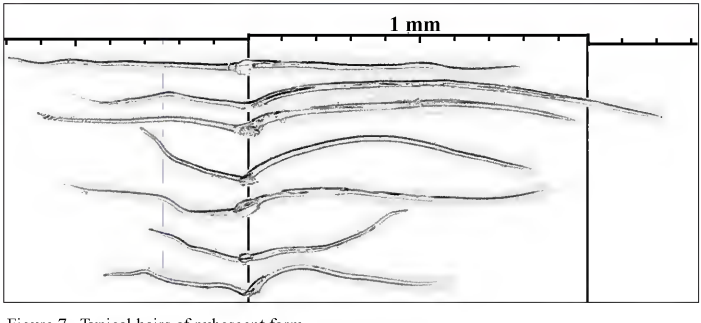


Figure 7. Typical hairs of pubescent form.

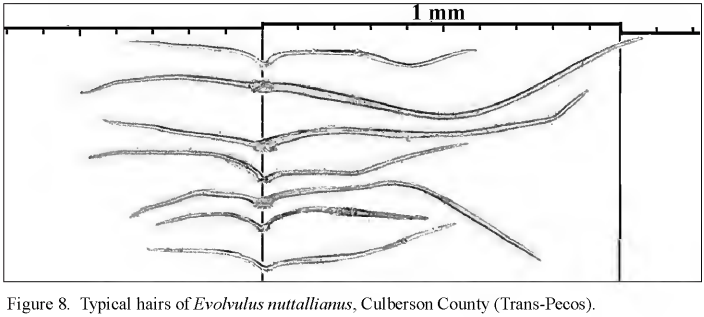


Figure 8. Typical hairs of *Evolvulus nuttallianus*, Culberson County (Trans-Pecos).

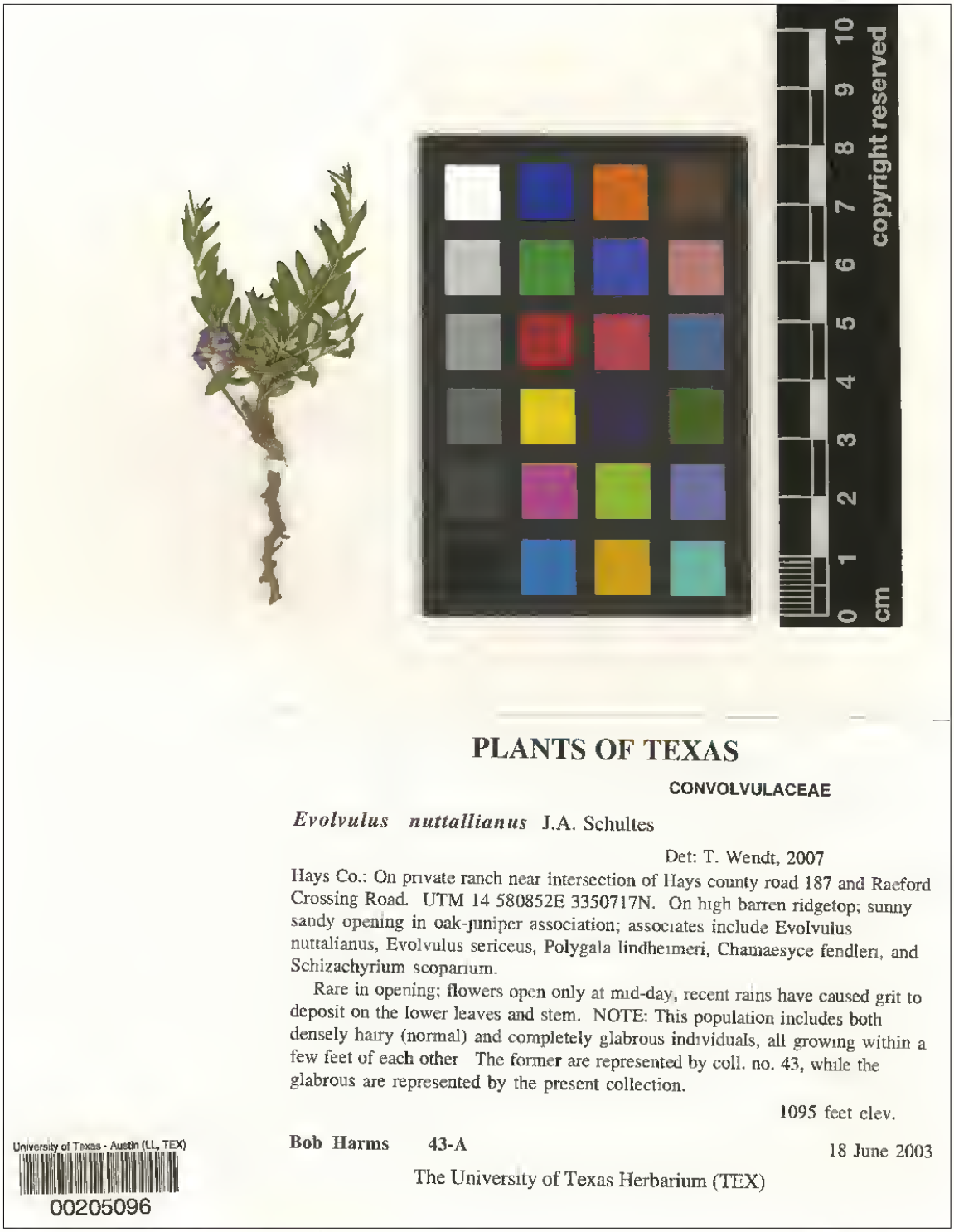


Figure 9. Glabrous *Evolvulus nuttallianus*, *Harms 43-A* [TEX], 18 Jun 2003 (cropped for figure display).

Figure 10. Glabrous *Evolvulus nuttallianus*, *Harms 43-A* [TEX], 18 Jun 2003 (scanned at 1200 dpi).

PLANTS OF TEXAS

CONVOLVULACEAE

Evolvulus nuttallianus J.A. Schultes

Det: T. Wendt, 2007

Hays Co.: On private ranch near intersection of Hays county road 187 and Raeford Crossing Road. . UTM 14 580852E 3350717N. On high barren ridgetop; sunny sandy opening in oak-juniper association; associates include Evolvulus nuttallianus, Evolvulus sericeus, Polygala lindheimeri, Chamaesyce fendleri, and Schizachyrium scoparium.

Rare in opening; flowers open only at mid-day; recent rains have caused grit to deposit on the lower leaves and stem. NOTE: This population includes both densely hairy (normal) and completely glabrous individuals, all growing within a few feet of each other. The former are represented by this specimen, while the glabrous are represented by coll. no. 43-A

1095 feet elev.

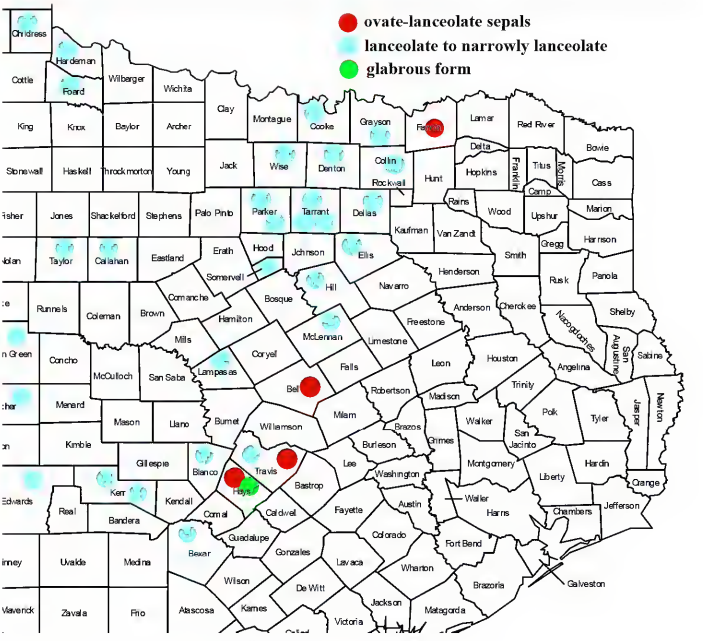
University of Texas - Austin (LL, TEX)

00205095

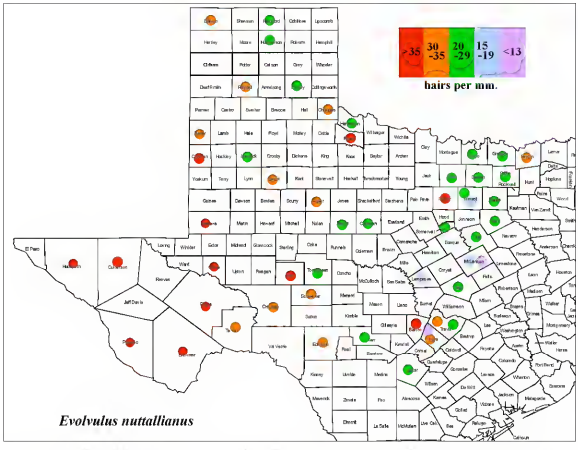
Bob Harms **43** 18 June 2003

The University of Texas Herbarium (TEX)

Figure 11. Pubescent *Evolvulus nuttallianus*, *Harms 43* [TEX], 18 Jun 2003 (cropped for figure display)



Map 1. Distribution of *Evolvulus nuttallianus* sepal types in the eastern half of Texas.



Map 2. Leaf hair density for *Evolvulus nuttallianus* in Texas, based on collections at TEX/LL and SRSC. No collections exist for Jeff Davis and Val Verde Counties.

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REPLY TO ANGELO: CHANGES IN THE FLORA OF CONCORD, MASSACHUSETTS

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Angelo (2014a, b) recently wrote two critiques of our research (work we did with several collaborators) documenting declines in the abundance of plant species in Concord, Massachusetts, and linking those changes in abundance with warming temperatures (Willis et al. 2008; Primack et al. 2009). We and our collaborators provided detailed responses (Primack et al. 2014; Willis & Davis 2014) to the first critique (Angelo 2014a). In his second critique, Angelo (2014b) added detail and new comments. Several points Angelo (2014b) makes have merit and suggest the need for a new formal flora of Concord. Further, his analysis has improved our data set. However, his main criticisms are based on misunderstandings of our goals, methods, and conclusions. Moreover, we believe our main findings — i.e., that many species in Concord, Massachusetts, are declining in abundance and that these changes in abundance are in part linked with warming temperatures — still hold true.

Our research (Willis et al. 2008; Primack et al. 2009) was not intended to produce a flora of Concord but rather to describe general patterns of change over time for a defined subset of plant species in Concord — i.e., species that past botanists such as Alfred Hosmer and Henry David Thoreau observed. Our community-level approach and statistical analysis allowed our results to be robust despite incomplete or imperfect information on individual species, including unclear taxonomy and other mistakes pointed out by Angelo (2014a, b) (some of which we think are valid, and some of which we disagree with). The "noise" that would have been caused by this imperfect information would have made it less likely that we would have detected the patterns that we did find — patterns that are consistent with results in many other locations.

In addition, our community-level approach — which was novel at the time — and our conclusions are consistent with the findings of others; our field and data-analysis methods are comparable to other field studies (e.g., Robinson et al. 1994; Leach & Givnish 1996; Lavergne et al. 2006). For example, other floras in urban and suburban areas of eastern Massachusetts have documented declines in the abundance of native species (Bertin 2002; Standley 2003), although the number of native species in Worcester County, a relatively large and rural area, does not appear to be declining (Bertin 2013). Studies in New England and a broader meta-analyses of over 1300 species responses globally have linked warming temperatures with shifts in species ranges (Beckage et al. 2008; Chen et al. 2011; Bertin 2013), and two separate meta-analyses have confirmed that changes in phenology are indeed linked with plant performance in many locations (Cleland et al. 2012; Wolkovich et al. 2013).

Below we provide brief responses to nine of the main points made by Angelo (2014b) about our work. For more detailed responses to most of these and other points, we refer you to our previous responses (Primack et al. 2014; Willis and Davis 2014).

1. Assertion: One of the early floras we used to assess changes in the abundance of plants included Concord and vicinity, whereas our surveys covered only Concord, creating a mismatch between the study areas.

Our response: We compared our survey results with data from three past botanical treatments, two of which were confined to Concord. Comparisons with all three show similar patterns of species decline.

2. Assertion: We did not thoroughly search of all of Concord; we did not search private, unprotected lands in particular; and we lacked the skill to find plants.

Our response: We thoroughly surveyed the plants of Concord over a five-year period. Our surveys involved several people searching for several days per week, with some additional fieldwork during the past seven years. We also sought advice from local botanists, including Angelo, about the locations of locally rare plants. We surveyed private and public lands, including private, unprotected areas. We have strong backgrounds in botany and have extensive experience of carrying out botanical surveys and statistical analysis.

3. Assertion: Some of species that we could not find do still occur in Concord, and some of the species are more common than we reported.

Our response: We have always acknowledged that additional fieldwork will result in people finding localities for populations we could not find (Primack et al. 2009). The additional locations reported by Angelo and others, some of which we have also found, represent a small percentage (less than 7%) of the species that we report as declining, and do not significantly affect the overall patterns in our findings.

4. Assertion: We cannot know the meaning of terms used by past botanists — i.e., what "common" or "occasional" meant in terms of absolute abundance. In particular, Hosmer (1903), one of the historical botanists we relied on in our study, was biased toward categorizing species as "common," whereas our undersampling biased us to categorize species as currently uncommon or rare. Thus, it was not surprising that we found that species were declining in abundance.

Our response: Even though past botanists did not define their terms for frequency of occurrence, it is reasonable to assume that individual botanists used the terms consistently, making our flora-wide comparative analysis of changes in *relative* abundance appropriate. Additionally, our results were consistent when comparing our survey results with those of three separate past botanical surveys, suggesting that our conclusions are not caused by a systematic bias between our survey and just one of the historical surveys.

5. Assertion: We erroneously assume that species found at just one site are invariably destined for extinction.

Our response: This is a misstatement of our conclusions. We are not stating that all rare species are destined for extinction. Rather, we simply point out that rare species or species with small populations face a much higher probability of local extinction, a basic tenant of population biology that has been confirmed by numerous studies.

6. Assertion: Accounting for factors other than climate change in our statistical analyses would reduce the relationship between climate change and declines in abundance that we found.

Our response: We used standard statistical analyses designed to account for the simultaneous effects of multiple ecological factors other than those associated with climate change, including habitat, deer browse preference, and status as a native or non-native species (Willis et al. 2010). Furthermore, we

made clear in our original discussion and our response that these additional factors have likely impacted the flora of Concord in conjunction with the effects of climate change.

7. Assertion: We found that populations appeared to decline most over the past 30-40 years, while temperatures did not warm substantially over that period compared to warming over the previous 100 years.

Our response: Population sizes do not have to fluctuate in synchrony with temperature for population decline to be related to temperature. In our case, we found an indirect relationship — species that declined tended to have flowering times that did not track changes in temperature and tended to have more northerly distributions. Bertin (2013) also found evidence of the effects of climate change, with northern species disproportionately declining in Worcester County. Even though temperatures have generally been warming in eastern Massachusetts for the past 160 years, the increases have been cumulative such that the past three decades have been the warmest overall, with many record high temperatures.

8. Assertion: We included inappropriate species in our study, including non-native species, species of uncertain taxonomy, and species known to be declining for reasons other than climate change.

Our response: Angelo (2014b) identified some problem species in our data set, which we are appreciative of. However, we disagree with many of his assessments regarding which species were appropriate to include or exclude. Given that our analysis took a community-level approach, and given that multiple factors can affect the abundance of a particular species simultaneously (e.g., deer grazing, air pollution, and a warming climate), we included all available species. We explicitly accounted for many factors that might affect their abundance — including non-native status, deer browse preference, and habitat — in our statistical analysis.

9. Assertion: If climate change were driving declines in the abundance of certain species, those declines would be widespread. However, many species that we found to be declining in abundance in Concord do not appear to be declining in abundance in two locations relatively close to Concord, the Middlesex Fells (Hamlin et al. 2013) and Worcester County (Bertin 2013), and therefor should be excluded from the analysis.

Our response: This is an interesting point. However, the abundance of each species is affected by many factors, and the balance of these factors varies from place to place (Cleland et al. 2012). In particular, each place has its own distinctive geology, soils, topography, history of past land use, and current intensity and types of human activity. Consequently, excluding species from our analysis of changes in abundance in Concord because they are not declining elsewhere is not appropriate.

Investigations of changes in the abundance of species are critical to conservation biologists and protected area managers charged with preserving biodiversity. Thus, we very much support continued investigations related to this topic and have made the data resulting from our work freely accessible for studies like those of Angelo (2014a, b) and others (e.g., Diez et al. 2012; Wolkovich et al. 2012; Wolkovich et al. 2013). In this case, Angelo (2014a, b) appears to agree that the number of native species in the Concord flora is declining, but he disagrees on the pace of the declines and the role of climate change. After considering his points, we find that our results are still valid, and his criticisms are based on a misunderstanding of our methods, goals, and statistical tests. More research, including a formal flora of modern Concord, if done, will continue to improve our understanding of how Concord's flora has changed since the observations of Thoreau and other botanists.

ACKNOWLEDGEMENTS

We appreciate generous help we received from local naturalists and botanists and others during the course of this project. We also thank Charlie Willis, Charles Davis, Brian Drayton, Libby Ellwood Amanda Gallinat, and Caitlin McDonough MacKenzie for their collaborations on this and related projects and for their comments on this response.

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FURTHER OBSERVATIONS ON RELATIONSHIPS IN THE *ERYTHRANTHE GUTTATA* GROUP (PHRYMACEAE)

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ABSTRACT

Sequence order in the DIV1 inversion region is known for four taxa of the *Erythranthe guttata* group and provides basis for an inference of relationship. One sequence order is found in *E. grandis* and *E. guttata*, which are rhizomatous perennials, the reverse order is found in *E. microphylla* and *E. nasuta*, which are non-rhizomatous annuals. Because annuals are the prevalent life form in sect. *Simiola* as well as among species regarded as most closely related to sect. *Simiola*, and because of the simple developmental origin of rhizomes, annuals are reasonably hypothesized to be the primitive form in sect. *Simiola*, with rhizomatous species evolutionarily derived from annuals. The DIV1 sequence in *E. grandis* and *E. guttata* is thus the inverted one — these two species either arose from a common ancestor with the distinctive inversion or else one species is derived from the other. Each of five suppositions underlying this hypothesis of relationship is discussed: (1) rhizomes are a derived feature in sect. *Simiola*; (2) the DIV1 inversion has occurred only once; (3) *E. nasuta* is distinct from *E. grandis-guttata-microphylla*; (4) *E. grandis* is a distinct entity, separate from *E. guttata* and *E. microphylla*, and (5) *E. guttata* in the strict sense and *E. microphylla* are distinct entities. Reference to these entities as "ecotypes" within a single species underemphasizes their degree of evolutionary independence.

A chromosomal inversion has been discovered among four monkeyflower species of sect. *Simiola* (Lowry & Willis 2010) — *Erythranthe nasuta*, *E. microphylla*, *E. guttata*, and *E. grandis* (Lowry and Willis identified each of the latter three as an "ecotype" within a broadly considered *Mimulus guttatus*). This inversion region (DIV1) is located on chromosome 8 (Linkage Group 8). Remarkably, the inversion sequence is perfectly correlated with the life history features of the four species — one sequence occurs in *E. guttata* and *E. grandis*, which are perennial and rhizomatous, occur in habitats with year-round moisture, and flower relatively late in the season, while the opposite sequence occurs in *E. nasuta* and *E. microphylla*, which are annual and slender-taprooted or fibrous-rooted, occur in quickly drying habitats, and flower in early season. These critical differences are guided by major QTLs localized on the DIV1 inversion region. The inversion, with its tightly linked, locally adaptive alleles, contributes to significant isolating mechanisms between species with contrasting sequences. All plants of a single population have the same sequence, thus the inversion is not a "polymorphism," as characterized by Lowry and Willis, at least not in the traditional sense of that term.

Holeski et al. (2014) have confirmed the existence of the LG8 inversion and also have identified two others — one on chromosome 5 and another on chromosome 10. Little is yet known about the effects of loci within these latter regions.

Friedman and Willis (2013) subsequently discovered another broad feature controlled in part from LG8 that is consistently characteristic of *Erythranthe guttata* and *E. grandis*: both have a short-day dependent, cold-chilling, vernalization requirement, while annuals (*E. microphylla*, *E. nasuta*, *E. lacinitata*, *E. pardalis*, and *E. mudata*) flower without vernalization. The difference in critical photoperiod is controlled by two, pleiotropic QTLs on LG8 — one of them appears to lie within the DIV1 inversion region. Differences in vernalization requirement are controlled by loci on LG 5, 6, 8, and 11 — Holeski et al. (2014) note that the LG5 marker resides within the chromosome 5 inversion identified in their study.

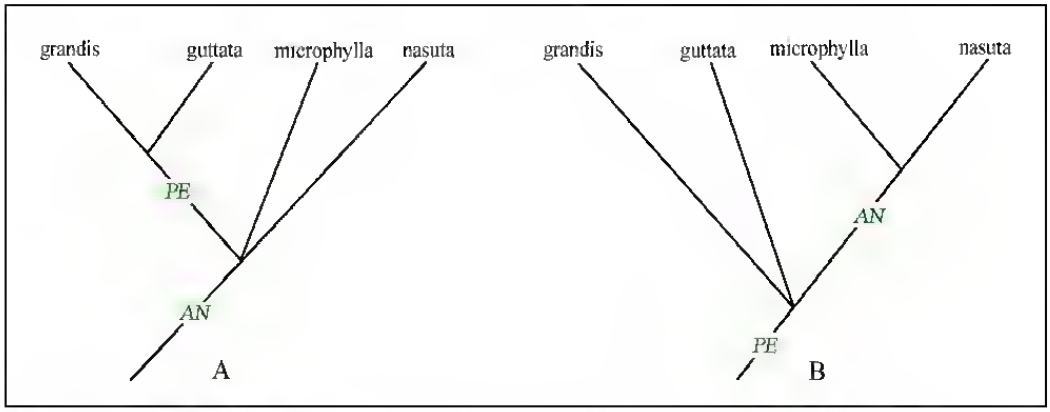

Figure 1 Cladistic distribution of the DIV1 inversion, as inferred from the sampling by Lowry & Willis (2010) A. If assumed that the DIV1 sequence in the annual taxa (AN) is the original state, that of the perennial taxa (PE) inverted, then *Erythranthe grandis* and *E. guttata* are sister taxa. B. If the perennial sequence were original, then *E. microphylla* and *E. nasuta* would be sisters.

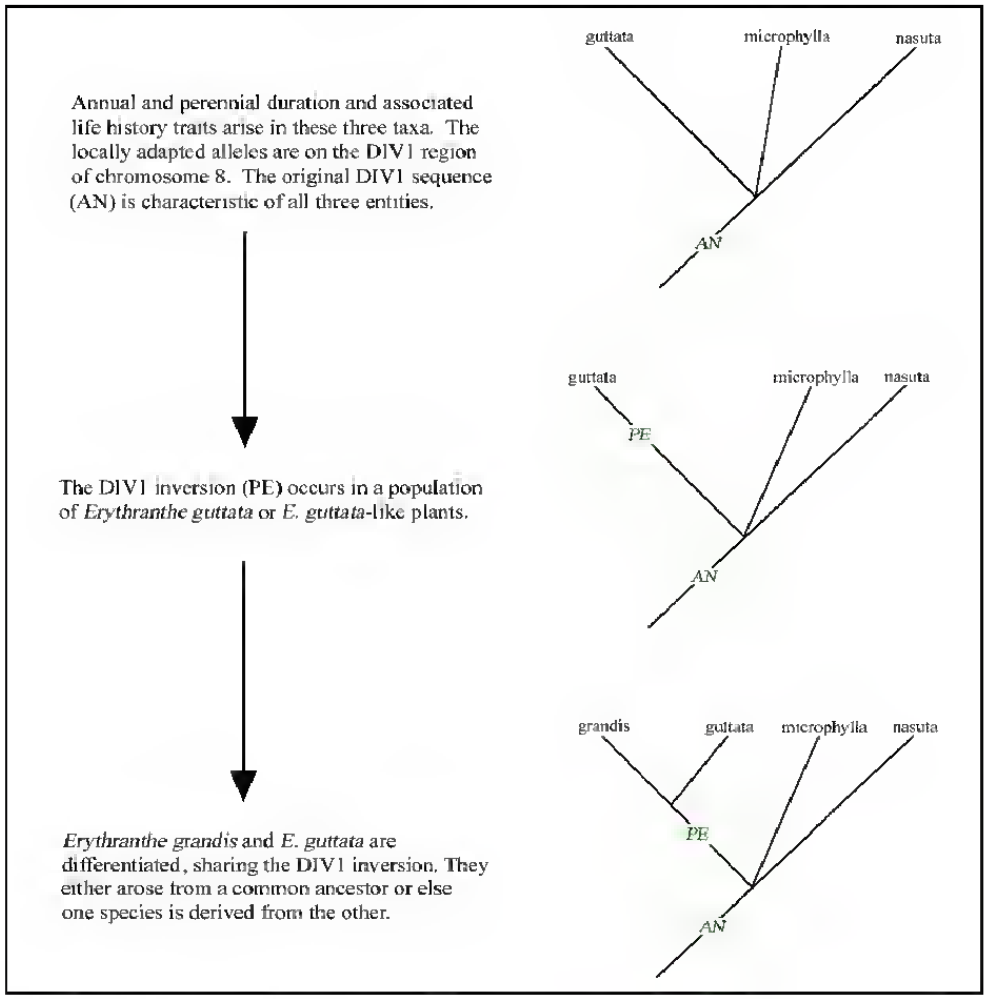

Figure 2 Origin and cladistic history of the DIV1 inversion, as hypothesized here for the four species studied by Lowry and Willis (2010).

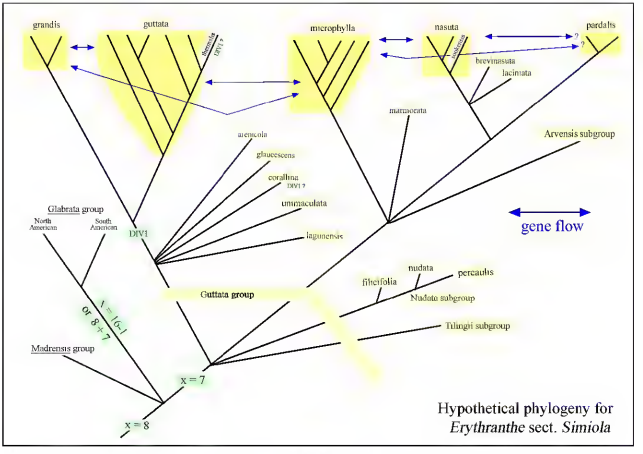

Figure 3 Hypothetical phylogeny of *Erythranthe* sect. *Simiola* (modified from Nesom 2013). Taxa of the Guttata group are highlighted in light yellow. Extra branches within *E. grandis*, *E. guttata*, *E. microphylla*, *E. nasuta*, and *E. pardalis* indicate the existence of regional variants. *Erythranthe grandis* and *E. guttata* share the DIV1 inversion sequence of chromosome 8, here interpreted as a derived feature. Apart from species of the *E. tilingii* subgroup, *E. corallina* is the only other perennial, rhizomatous species of the Guttata group. *Erythranthe thermalis*, an annual, is derived directly from perennial *E. guttata* and would be expected to have the inverted sequence. The hypothesized 'microphylla-nasuta-pardalis' clade perhaps will prove to be without synapomorphic justification — it is depicted here as a clade to emphasize the observation that all included species are annual (but annual duration is hypothesized to be plesiomorphic in this group).

It is hypothesized here that annual duration (vs. perennial) is the primitive state in *Erythranthe*, with rhizomatous species evolutionarily derived from the annuals — the perennial DIV1 sequence is thus the inverted one. The derived features shared by *E. guttata* and *E. grandis* were either inherited from a recent common ancestor with the distinctive inversion or else one of the species is derived from the other (Fig. 1). A generalized series of events leading to the distribution of the inversion sequences is hypothesized in Figure 2. Evolutionary origin of at least some of the locally adapted alleles almost certainly preceded the occurrence of the inversion.

The hypothesis of relationship presented here makes five suppositions.

1. **Rhizomes are a derived feature in sect. *Simiola*.** The comments below are from Nesom (2014).

"Evolutionary change from perennial (rhizomatous) to annual and from annual to perennial apparently has occurred multiple times among species of *Erythranthe* (as well as in the Phrymaceae as a whole). It is suggested here that rhizomes and stolons in *E. guttata*, *E. corallina*, and *E. grandis* and in the *E. tilingii* group probably are derived features, arising from ancestors of annual duration.

All other x = 7 sect. *Simiola* species are annual, without rhizomes or stolons, as are most other species of *Erythranthe*. See related earlier comments (Nesom 2012)."

"Conceivably it is developmentally simple for lower branches to become rhizomelike or stolonlike by production of adventititous roots. Plants of *Erythranthe arvensis* and *E. cordata* characteristically are of annual duration (without rhizomes or stolons), but large plants in wet habitats sometimes become proximally decumbent or prostrate and develop adventitious roots at lower nodes and along the internodes. *Erythranthe glaucescens* is characteristically annual, but at least one rhizomatous population is known (Nesom 2012, p. 61; Taylor 2013) — the rhizomes (or runners) either arising independently from within the species or perhaps their genetic basis acquired by hybridization with *E. guttata*. Given the topology of Figure 1 [= Figure 3 in the present discussion], it is likely that the rhizomes of *E. tilingii*, *E. guttata*, and *E. corallina* are not strictly homologous but rather have arisen independently in each instance."

Species indicated at present to be evolutionary sister groups to sect. *Simiola* (sect. *Exigua*, with the single species *E. exigua*, and the sister pair sect. *Mimulosma* with 20 species and sect. *Mimulasia* with 11 species; Beardsley et al. 2004) mostly are annuals. Some species of sects. *Mimulosma* and *Mimulasia* are rhizomatous, but the same rationale applies to them — rhizomes probably are derivative.

2. **The DIV1 inversion has occurred only once.**

This is first an argument from parsimony. Origin of the DIV1 inversion through a single event is a simpler assumption than one of its independent occurrence in two otherwise very similar species. Biologically as well, independent occurrences and selection of an identical inversion are improbable.

3. ***Erythranthe nasuta* is distinct from *E. grandis-guttata-microphylla*.**

In addition to its distinct morphology, ecology, and life history (e.g., Benedict et al. 2012; Nesom 2012), molecular-genetic studies also have shown *Erythranthe nasuta* to be distinct from *E. grandis*, *E. guttata*, and *E. microphylla* (e.g., Sweigart & Willis 2003; Sweigart et al. 2008; Oneal et al. 2014). In the Oneal et al. analysis, *E. nasuta* and *E. laciniata* are closely similar to each other and distinct from all the other taxa in markers from the inverted region of LG8; in the whole genome markers (outside of DIV1, K=4 through K=8), the two are distinct from each other and each also is unambiguously distinct from all other taxa.

Erythranthe nasuta and *E. microphylla* are broadly sympatric and natural hybrids between them are common. Introgression occurs between the two, though it is mostly unidirectional, into *E. microphylla* (Sweigart & Willis 2003; Martin & Willis 2007). Intrinsic postzygotic isolation exists (moderate F1 hybrid inviability with *E. microphylla* as seed parent) but is weak compared to prezygotic isolation — this, however, has not constrained the consistent recognition of *E. nasuta* as a distinct species (see related comments below regarding recognition of *E. grandis*, *E. guttata*, and *E. microphylla*).

4. ***Erythranthe grandis* is a distinct entity, separate from *E. guttata* and *E. microphylla*.**

Erythranthe grandis is a distinct species (e.g., Nesom 2012, where it is analogous in concept to others, based on morphology and geography) and differences between it and *E. microphylla* in morphology, ecology, and genetics are documented in a series of studies comparing the "coastal perennial form of *Mimulus guttatus*" (= *E. grandis*) to the "inland annual form" (= *E. microphylla*) (Hall & Willis 2006; Lowry et al. 2008; Lowry et al. 2009; Hall et al. 2010; Lowry & Willis 2010). "Coastal perennial and inland annual populations of *M. guttatus* comprise two distinct morphologically and molecular genetically diverged groups. Nearly complete prezygotic isolation through a combination of geography, selection against immigrants, and flowering time isolation likely

maintains the genetic differentiation of these coast and inland groups" (Lowry et al. 2008, p. 2209). Lowry et al. (2009) further found in reciprocal transplant studies that alleles of *E. grandis* at three salt spray tolerance loci are adaptive in the coastal perennial habitat but are not significantly disadvantageous in the inland annual habitat.

Erythranthe grandis also has been shown as genetically discrete within a sampling of sect. *Simiola* that included *E. guttata* (the "inland perennial"), *E. microphylla*, *E. nasuta*, *E. laciniata*, *E. nudata*, *E. tilingii*, and perhaps others. A neighbor-joining tree of these taxa based on *m*AP3 sequences shows a strongly supported cluster of five *E. grandis* samples from Marin Co. in central California to Lane Co. in central Oregon (Sweigart & Willis 2003, Group P in their Figure 3, 100% bootstrap support). Coastal perennials from California and Oregon also cluster together in the study by Oneal et al. (2014).

Lowry et al. (2008, p. 2211) noted that "Although our results demonstrate essentially complete prezygotic isolation and suggest that the coastal perennial and inland annual races of *M. guttatus* are in fact distinct biological species, the process by which most ecological races form, maintain their genetic distinctness, and accumulate further reproductive isolating barriers remains poorly understood." They were not explicit as to why they did not, in fact, regard *Erythranthe grandis* and *E. microphylla* as distinct species, but comments in their next paragraph (p. 2211) are closest to a statement in this whole series of studies regarding what further is necessary, in their opinion, for the speciation process to be completed. Apparently it is that "additional reproductive isolating alleles [must] spread between races" — i.e., "genic incompatibilities [that] are frequently involved in intrinsic postzygotic isolation" and which "facilitate the conversion of ecological races into good species." Thus in these monkeyflowers, following Lowry's review (2012) of stages in species formation, until the speciation process is 'irreversible,' they are considered ecotypes of a single species. One might have expected that discovery of the DIV1 inversion would be seen as a genic incompatibility contributing to irreversibility, but molecular-geneticists continue to regard "*Mimulus guttatus*" as comprising at least three "ecotypes."

In sum, *Erythranthe grandis* and *E. microphylla* are distinct in morphology, phenology, ecology, and genetic constitution, the two are nearly completely reproductively isolated (prezygotically), and a chromosome repatterning preserves the coherence of a suite of traits critical to their distinction. Reference to these entities as "ecotypes" of a single species underemphasizes their degree of evolutionary independence and does not account for their apparent cladistic history (they are not sister taxa nor does it seem probable that one is derived from the other). If the choice of terms is seen as essentially arbitrary (as reference to a particular point in a continuous speciation process), "species" is more accurate because what is meant by "ecotype" encompasses a much broader range of conditions and is correspondingly much more vague. Even if these entities have not achieved 'full' species status, as implied by Lowry and Willis (but which clearly is an arguable idea), they are much closer to that endpoint than to the beginning point of ecotypic differentiation.

The "inland perennial form of *Mimulus guttatus*" (= *Erythranthe guttata* in the strict sense) was <u>not</u> included in the series of molecular-genetic studies of *E. grandis*/*E. microphylla*, but compared to the annuals, plants of strict *E. guttata*, like *E. grandis*, also occur in a markedly different habitat (permanent water) and begin flowering considerably later. Recognition of reproductive isolation between *E. guttata* and *E. microphylla* completes a view of their relationship as analogous to that between *E. grandis* and *E. microphylla*.

Strict *Erythranthe guttata* and *E. grandis* are morphologically distinct between themselves and samples of inland perennial *E. guttata* were included in both Sweigart and Willis (2003) and Oneal et al. (2014), as noted above, where *E. grandis* formed a closely coherent cluster. In the hypothesis here, *E. guttata* and *E. grandis* are evolutionary sister taxa. Perhaps the most interesting

experimental contrast within this small group of species remains to be done — between *E. guttata* and *E. grandis*.

The immediate ancestor of *Erythranthe grandis/guttata* may have been a population of *E. microphylla*-like plants, especially in view of the sympatry and demonstrated genetic overlap between *E. guttata* and *E. microphylla*. On the other hand, the annual *E. unimaculata* also is partially sympatric with *E. guttata* and otherwise bears a strong resemblance to it — it should reasonably be considered among possible progenitors. Morphological similarities of the annual *E. glaucescens* to *E. guttata* imply that an understanding of its evolutionary origin also may influence the interpretation of the relationship between *E. microphylla* and *E. guttata*. Similarly, study of *E. arenicola* may prove to have a direct bearing on such interpretations. And should the rhizomatous *E. corallina* prove to have the DIV1 inversion, such might imply that *E. microphylla* was even further removed from immediate ancestry of *E. grandis/guttata*.

Geographic variation exists within *Erythranthe grandis*. Plants from Oregon commonly produce nearly orbicular leaves and the stems tend to lie flat and produce adventitious roots along the prostrate portions. In the extreme, such plants are highly distinctive, even to the point that I once thought that they might deserve formal taxonomic recognition. Whether this form intergrades completely with the more guttata-like morphology (oblong leaves, erect stems) of southern *E. grandis* remains to be investigated.

5. ***Erythranthe guttata* in the strict sense and *E. microphylla* are distinct entities.**

With knowledge that the DIV1 inversion provides coherence for loci underlying a strong reproductive barrier between *Erythranthe grandis* and *E. microphylla*, it seems evident that a similar relationship exists between *E. guttata* and *E. microphylla*, which are distinct in morphology, habitat, phenology, and genetics. "Annual *M. guttatus* are nearly entirely distinct from perennial *M. guttatus* [including inland populations], although a few annual and perennial *M. guttatus* from California share some variation" (Oneal et al. 2014, p. 2581). Evidence perhaps exists for "limited introgression" in the inversion but most of the shared variation apparently is underlain by genetic similarities in the non-inversion regions, presumably reflecting the influence of gene flow, perhaps coupled with parallel selection. This shared, whole-genome variation presumably is what underlies the observation that "Published gene trees show *M. guttatus* to be a polytomy of annuals and perennials (Oneal et al. 2014, p. 2854).

Lowry and Willis (2010) described the geographic distribution of the DIV1 inversion as a mosaic of patchily distributed (corresponding to habit) annual and perennial populations of "*Mimulus guttatus*." The same concept is expressed by noting that *E. guttata* and *E. microphylla* occur as two species in close sympatry with distinctions maintained by reproductive isolation.

In the concept of current molecular-geneticists, "*Mimulus guttatus*" occurs both in annual and perennial ecotypes (e.g., Lowry et al. 2009; Lowry & Willis 2010; Oneal et al. 2014). In contrast, recognized species, across all genera and families, that are characterized by a mix of annual and perennial populations are rare or perhaps nonexistent (the rhizomatous population of *Erythranthe glaucescens*, noted above, is exceptional). Moyers and Rieseberg (2013) described populations of perennial plants as an ecotype within the otherwise annual species *Helianthus annuus* — these populations, however, are geographically localized, have other divergent characters (morphology, phenology, chemistry), and have been subsequently been formally recognized at specific rank (Stebbins et al. 2013). Some perennials may occasionally flower at a young age and thus might appear to be annual if observed only in that short moment of time, but this is not the case in monkeyflowers. Some perennial species may have rhizomatous and non-rhizomatous forms, but in the few such cases that I am aware of, there is a clear geographic distinction between the two forms. Among flowering plant species, annual and perennial duration generally appear to be regions of

evolutionary stability, and the argument here removes a broadly considered "*Mimulus guttatus*" from consideration as a possible exception.

With reference to the *Erythrathe guttata* species group, Oneal et al. (2014, p. 2857) noted that "Our results suggest that even though considerable phenotypic differentiation exists between identifiable 'species,' there also exists **extensive shared neutral genetic variation across the complex** [emphasis added], which may ultimately undermine any clear taxonomy of the group. This common genetic variation is probably the result of shared ancestral polymorphism or ongoing gene flow, which has occurred despite high levels of reproductive isolation ... between members of the complex." This is perhaps not a particularly remarkable observation, because in common parlance the "extensive shared neutral genetic variation across the complex" surely mirrors the idea that they are members of the same genus (i.e., that the "shared neutral genetic variation" indeed is "shared ancestral polymorphism"). Such probably is the case in many genera, particularly those that are relatively recently evolved and characterized by many species separated by small differences.

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JOHN LAWSON'S PLANT COLLECTIONS, VIRGINIA AND NORTH CAROLINA 1710-1711

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ABSTRACT

John Lawson, surveyor-general of Carolina, published a well-known travelogue and natural history called *A New Voyage to Carolina* in 1710. He also sent numerous herbarium specimens to James Petiver in London. Petiver's collections ended up in Hans Sloane's herbarium, where they are now part of the Sloane Herbarium in the Natural History Museum, London. We have digitally photographed these specimens and placed them online as part of the Botanica Caroliniana project. Here we present determination of the taxa in Lawson's collections along with observations on Lawson's movements and other work.

John Lawson was one of the great early explorers of North America. Between 1700 and 1711 he visited and mapped a good portion of the colony then called Carolina, staying with Indians and watching his colleagues' exploits with amusement. He turned this experience into both a good job — surveyor-general of Carolina — and a bestselling 1710 travel memoir, *A New Voyage to Carolina*. He even died a glamorous — albeit unpleasant — death, captured and executed by Indians.

He was also quite a good botanist. This is evident in *A New Voyage*, which is full of descriptions of plant species, both their appearances and their uses. Lawson was one of the new breed of scientist that appeared in the late 17th and early 18th century — an amateur who believed that he could contribute to new efforts to catalog the world's contents. Lawson and other individuals like him collected specimens and observations wherever they were and sent their findings back to centers in Europe (Stearns 1952). These "centers" were typically individuals with a penchant for collecting. Later in the 1700s, Carl Linnaeus used this method to assemble the collections that formed the basis of his *Systemae Naturae*. Linnaeus's students sailed the world, sometimes dying in the process, and sent scores of dried plants and other specimens back to Uppsala (Linnean Society 2013). The process was similar to crowdsourcing, with the contributors functioning as remote data collectors.

Lawson worked on a similar earlier project that never became as famous as Linnaeus' but that still has great value today. His dried plant specimens still survive in the Sloane Herbarium of the

Natural History Museum London. This is largely due to his relationship with his own "Linnaeus," James Petiver (Stearns 1952).

James Petiver: Apothecary and publisher

James Petiver was an apothecary who kept a shop "at the sign of the White Cross in Aldersgate Street" in London. He was also an amateur scientist, keen to capitalize on the potential of the ships that were now sailing in every direction from England carrying scientists, ministers, physicians, politicians, and people who hoped to find their fortunes in other lands. These adventurers also happened to be a great source of data in the form of new plants and animals in the Americas and Asia (Stearns 1952).

Petiver was one of the first members of the Royal Society, which formed around 1689, initially as a club of natural philosophers who met on Friday evenings to exchanged specimens and discuss botany. Hans Sloane, just back from 15 months in Jamaica, was one of the founding members. Other members included William Sherard, Samuel Doody, Samuel Dale, Charles du Bois, Leonard Plukenet, and Adam Buddle (Stearns 1952).

Petiver never attended a university, and he could not read modern European languages, though he could read and write Latin. His apothecary practice kept him quite busy, and he left hundreds of pages of notes on his treatment of various patients. It seems likely that his interest in botany came out of his profession; apothecaries used many medicinal plants and Petiver and his colleagues spent a good deal of time "botanizing" and visiting collections of medicinal plants (Stearns 1952).

Around 1690 Petiver began corresponding with scientists who had visited or were living in other locations. Initially he wrote to individuals he met through the Royal Society and then gradually expanded this network to anyone who would make collections and send them to him. Over the years a number of men took the trouble to collect specimens, pack them carefully, and ship them to London (Stearns 1952).

Petiver used this correspondence as the basis for a series of publications called *Musei Petiverani Centuria Prima Rariora Naturae Continens*, short books on natural history that he began producing in 1695. These books contained the names and descriptions of plants, animals, and shells that had been sent to him from locations such as Africa, China, Barbados, Cartagena, and Norway. He credited the individuals who had sent him the objects and concluded his volumes with a solicitation for contributions from others. Contributions were to be sent to his shop in Aldersgate Street (Stearns 1952) .

Over the next decade, contributors sent Petiver more and more collections of natural history specimens. Petiver provided some of them supplies such as brown paper, bottles, packing lists, and instructions on how to preserve fleshy bodies and collect plant specimens. He told his contributors that whenever they went on shore they should bring with them a collection book, an insect box, paper bags, and pins, and to collect whatever butterflies and moths, fruits and berries, shells, and anything else they found, taking care not to break the brittle pieces (Stearns 1952).

In exchange for their contributions, Petiver served as a source of valuable information for his correspondents. He sent them journals and books, scientific instruments, and answered their questions. In the case of Joseph Lord, he seems to have served as a vital source of communication, perhaps an intellectual lifeline for an educated man living in the wilderness of South Carolina (Blackwell and McMillan 2013). He sometimes reimbursed contributors for expenses incurred in making collections. For the most part, however, Petiver promised his contributors fame as

compensation for their work. This was sufficient to persuade many individuals to send him numerous collections (Stearns 1952).

The Carolinas were an especially rich source of contributions for Petiver. His contributors from the region included Major William Halsteed, Robert Ellis, George Francklin, and Edmund Bohun, all of whom collected in the Charleston area around 1700 (Dandy 1958). They also included John Lawson.

John Lawson: Author, adventurer, and real estate developer

Little is known about John Lawson's background. Stearns suggests that he might have been an apothecary, based on his connection with Petiver, his interest in botany, and a 1675 entry in the books of the London Society of Apothecaries mentioning "John Lawson, son of Andrew Lawson, Citizen & Salter of London, examined, approved & bound to John Chandler for 8 years" (Stearns 1952). Other accounts put Lawson's birth too late for that entry to refer to him. The Dictionary of North Carolina Biography lists his birth date as 27 December, 1674, and his parents as Dr. John Lawson and Isabella Love. Dr. Lawson owned estates in Yorkshire, where his son grew up (DocSouth 2014).

In any case, Lawson sailed to Carolina in 1700, arriving in Charleston late in the year. On December 28, 1700, he and a group of Virginia traders and native Americans set out on a journey through the backcountry of what is now North Carolina. The Lords Proprietor assigned him the task of mapping and surveying the interior of the territory (Bellis 2007).

Lawson's group followed the Santee and Wateree Rivers northwest through South Carolina and the followed the Trading Path used by Indians north and east through the interior of North Carolina. There they crossed the Eno River near Durham, crossed the falls of the Neuse River, and entered Tuscarora territory. Accompanied by some Tuscarora Indians, they made their way to the site of present-day Greenville and then came to the English settlements on the Pamlico River.

At the conclusion of his journey, Lawson built himself a house in what became the town of New Bern. In 1706 he participated in the foundation of the town of Bath. He spent much of the decade surveying the land around Bath, eventually becoming surveyor-general of Carolina (Bellis 2007).

Lawson had kept a detailed journal during his journey through Carolina, recording both human events and descriptions of nature. He used these notes as the basis of his popular 1709 travelogue, *A New Voyage to Carolina*. This book was a tremendous success and persuaded many immigrants to move to Carolina from Europe, perhaps one of Lawson's goals in publishing it. The book is still a good read today and remains justifiably popular among fans of North Carolina history.

Lawson had first written Petiver in 1701, responding to one of Petiver's advertisements seeking plant and animal specimens. This seems to have led to nothing, but in 1709 Lawson met Petiver in person when he traveled to London to oversee the publication of his book. Petiver was quite impressed with the book, particularly with Lawson's treatment of trees. Petiver gave Lawson supplies and asked him to send specimens after he returned to Carolina. He also gave him grape vines, some apothecary materials and collecting supplies, and a copy of John Ray's book on Virginia plants (Bellis 2007; Stearns 1952).

Lawson returned to North Carolina in early 1710, accompanied by several hundred Germans who intended to settle property Lawson owned on the Neuse River, near the house he built after his journey in 1700. This settlement became the town of New Bern (Bellis 2009).

Lawson's group landed in Norfolk, Virginia, in April and spent a month held by French privateers. After the French released them, Lawson and his colonists traveled south toward New Bern. On this journey Lawson began assembling the collection of plants that survives in the Sloane Herbarium, collecting plants as he led his settlers to their new home. He spent four months in the spring of 1711 exploring the Pamlico peninsula, taking cuttings and writing short notes that included collection dates, locations, and sometimes brief descriptions. The first packet of specimens went out to Petiver in July 1710, followed by another in July 1711. Lawson also sent Petiver a letter in which he described his plans to produce a complete natural history of Carolina, in which he would describe all the plants he could find as well as beasts, birds, fishes, insects, fossils, soils, and the weather (Bellis 2009). Lawson's handwritten notes accompanying the specimens include numerous references to pages and lines in his *A New Voyage*; it appears that he was attempting to collect the plants that he had already described in his publication. Perhaps this was meant as preparation for his next work or simply as vouchers for the taxa he had already observed.

Lawson's natural history was not to be. He took his last journey up the Neuse in the fall of 1711, along with the German Christopher von Graffenried, one of the founders of New Bern. The two were captured by Tuscarora Indians. The Indians released van Gaffenried but killed Lawson on September 22 (Stearns 1952). Christopher Gale reported that Lawson was executed in a manner described in *A New Voyage*, stuck with splinters of torch wood and set afire. Van Graffenried did not know; he had heard that Lawson's throat had been cut with his own razor or that he had been hung or burnt (Lawson & Lefler 1967).

Petiver died in 1718 and Hans Sloane purchased his collections. Sloane's collections eventually formed the original collections of the British Museum (Dandy 1958).

Identification

Dandy lists Lawson's specimens as occurring in several volumes in the Sloane Herbarium: H.S. 145, ff. 45-66; H.S. 242, ff. 110-136; H.S. 171, f. 65; H.S. 158, ff. 129, 151, and 214; and H.S. 159, ??? (Dandy 1958). "H.S." is an abbreviation for "Herb. Sloane" and is the term used to refer to all the volumes in the Sloane collection. Other authorities claim that it is an abbreviation for "Hortus siccus," but that is incorrect in this case. The "f." used to mark pages is an abbreviation for "folio," the Latin word for "page."

We photographed all of these pages as part of our initial work on the Botanica Caroliniana project in November, 2012. We have posted images of all of Lawson's specimens on the Botanica Caroliniana website (Hackney, Blackwell, & Blackwell 2013).

Vincent Bellis, professor emeritus at East Carolina University, has worked with the Lawson specimens for years. In 2009 he published an article in *Castanea* in which he identified taxa found in these collections and provided a detailed analysis of Lawson's movements and likely collection locations. This article was based on examination of digital images at East Carolina University in their Digital Collections (John Lawson, Naturalist 2014). Bellis's geographical analysis and historical description are excellent, and we have not attempted to add to them.

McMillan and Hackney Blackwell identified the specimens in Lawson's collections using the same methods we employed with the Mark Catesby materials, examining the high-resolution digital images and referring to online flora and images (McMillan et al. 2013; McMillan & Blackwell 2013; Blackwell & McMillan 2013). All determinations are based on Alan Weakley's 2012 *Flora of the Southern and Mid-Atlantic States* (Weakley 2012).

RESULTS

We present two separate lists of determinations: one by volume and folio, and one by taxa organized by family. Most of these specimens are confirmed as Lawson's by Dandy; a few in H.S. 159 are specimens we suppose are Lawson's, based on the handwriting of the accompanying labels.

Determinations by volume and page

Volume and page	Position on page	Species	Family
H.S. 145 f. 45	bottom second from right	*Helianthus divaricatus* L.	Asteraceae
H.S. 145 f. 45	upper right	*Liatris squarrosa* (L.) Michx.	Asteraceae
H.S. 145 f. 45	Second from bottom left	*Cyperus echinatus* (L.) Wood	Cyperaceae
H.S. 145 f. 45	bottom right	*Euphorbia pubentissima* Michx.	Euphorbiaceae
H.S. 145 f. 45	second from right	*Desmodium tenuifolium* Torrey & A. Gray	Fabaceae
H.S. 145 f. 45	second from left	*Galactia regularis* (L.) B.S.P	Fabaceae
H.S. 145 f. 45	bottom left	*Galactia regularis* (L.) B.S.P	Fabaceae
H.S. 145 f. 45	upper left	*Coreopsis tripteris* L.	Asteraceae
H.S. 145 f. 46	bottom left	*Onosmodium virginianum* (L.) A.DC (=*Lithospermum virginianum* L.)	Boraginaceae
H.S. 145 f. 46	top right	*Cyperus* sp.	Cyperaceae
H.S. 145 f. 46	top left	*Chamaecrista fasciculata* (Michx.) Greene	Fabaceae
H.S. 145 f. 46	top middle	*Rhynchosia difformis* (Ell.) D.C.	Fabaceae
H.S. 145 f. 46	bottom right	*Rhynchosia tomentosa* (L.) Hook. & Arn.	Fabaceae
H.S. 145 f. 47	top right	*Lyonia mariana* (L.) D. Don	Ericaceae
H.S. 145 f. 47	bottom right	*Lyonia mariana* (L.) D. Don	Ericaceae
H.S. 145 f. 47	top left	*Lilium superbum* L.	Lilliaceae
H.S. 145 f. 47	second top	*Platanthera ciliaris* (L.) Lindley	Orchidaceae
H.S. 145 f. 47	bottom left	*Agalinis setacea* (J.F. Gmel.) Raf.	Orobanchaceae
H.S. 145 f. 47	bottom middle	*Pleopeltis polypodioides* (L.) E.G. Andrews & Windham subsp. *michauxiana* (Weatherby) E.G. Andrews & Windham	Polypodiaceae
H.S. 145 f. 47	far right	*Verbena carnea* Medik.	Verbenaceae
H.S. 145 f. 48	bottom left	*Hieracium* sp.	Asteraceae
H.S. 145 f. 48	top right	*Symphyotrichum* sp.	Asteraceae
H.S. 145 f. 48	fern	*Pteridium aquilinum* (L.) Kuhn	Dennstaedtiaceae
H.S. 145 f. 48	top left	*Vaccinium formosum* H.S. Andrews	Ericaceae
H.S. 145 f. 48	bottom second from left	*Clitoria mariana* L.	Fabaceae
H.S. 145 f. 48	top center	*Tephrosia spicata* (Walt.) Torrey & A. Gray	Fabaceae
H.S. 145 f. 48	bottom flower	*Sabatia* sp. (*Sabatia campanulata* (L.) Torrey?)	Gentianaceae
H.S. 145 f. 48	bottom right	*Oenothera fruticosa* L.	Onagraceae
H.S. 145 f. 49	top third from left	*Ruellia caroliniensis* (J.F. Gmel.) Steud.	Acanthaceae

H.S. 145 f. 49	bottom fragment	*Sambucus canadensis* L.	Adoxaceae
H.S. 145 f. 49	top left	*Chrysopsis mariana* (L.) Ell.	Asteraceae
H.S. 145 f. 49	center	*Cyrilla racemiflora* L.	Cyrillaceae
H.S. 145 f. 49	top fourth from left	*Amphicarpaea bracteata* (L.) Fernald	Fabaceae
H.S. 145 f. 49	bottom second from right	*Hylodesmum nudiflorum* (L.) H. Ohashi & R.R. Mill (= *Desmodium nudiflorum* (L.) DC)	Fabaceae
H.S. 145 f. 49	top second from left	*Aureolaria virginica* (L.) Penn.	Orobanchaceae
H.S. 145 f. 49	top right	*Aureolaria virginica* (L.) Penn.	Orobanchaceae
H.S. 145 f. 49	bottom right	*Penstemon* sp.	Plantaginaceae
H.S. 145 f. 49	bottom left	*Thalictrum thalictroides* (L.) Eames & Boivin	Ranunculaceae
H.S. 145 f. 50	bottom right	*Eutrochium dubium* (Willd. ex Poir.) E.E. Lamont	Asteraceae
H.S. 145 f. 50	top left	*Taxodium distichum* (L.) L.C. Richard	Cupressaceae
H.S. 145 f. 50	center top	*Cyrilla racemiflora* L.	Cyrillaceae
H.S. 145 f. 50	bottom center right	*Desmodium paniculatum* (L.) DC	Fabaceae
H.S. 145 f. 50	top right	*Cypripedium parviflorum* Salisb. var. *pubescens* (Willd.) Knight	Orchidaceae
H.S. 145 f. 50	bottom center left	*Hexalectris spicata* (Walt.) Barnhart	Orchidaceae
H.S. 145 f. 50	bottom left	*Maianthemum racemosum* (L.) Link	Ruscaceae
H.S. 145 f. 51	top left	*Eutrochium dubium* (Willd. ex Poir.) E.E. Lamont	Asteraceae
H.S. 145 f. 51	bottom left	*Tillandsia usneoides* (L.) L.	Bromelliaceae
H.S. 145 f. 51	Right	*Scirpus cyperinus* (L.) Kunth	Cyperaceae
H.S. 145 f. 52	bottom left	*Liatris squarrosa* (L.) Michx.	Asteraceae
H.S. 145 f. 52	top left	*Scirpus cyperinus* (L.) Kunth	Cyperaceae
H.S. 145 f. 52	bottom center	*Decodon verticillatus* (L.) Ell.	Lythraceae
H.S. 145 f. 52	Right, with seeds in corner	Poaceae sp.	Poaceae
H.S. 145 f. 53	top left	*Vernonia acaulis* (Walt.) Gleason	Asteraceae
H.S. 145 f. 53	top center	Poaceae sp.	Poaceae
H.S. 145 f. 53	right	*Zizania aquatica* L. var. *aquatica*	Poaceae
H.S. 145 f. 54	top right, bottom right, center right	*Ageratina altissima* King & H. Rob. var. *altissima*	Asteraceae
H.S. 145 f. 54	left	*Decodon verticillatus* (L.) Ell.	Lythraceae
H.S. 145 f. 54	top center	*Chasmanthium sessiflorum* (Poir.) Yates	Poaceae
H.S. 145 f. 55	bottom center	Indet.	
H.S. 145 f. 55	top	*Apios americana* Medik.	Fabaceae
H.S. 145 f. 55	bottom left and right	*Lilium michauxii* Poir.	Liliaceae
H.S. 145 f. 56	bottom right three	*Apios americana* Medik.	Fabaceae

H.S. 145 f. 56	top left	*Nyssa sylvatica* Marsh.	Nyssaceae
H.S. 145 f. 57		*Magnolia tripetala* (L.) L.	Magnoliaceae
H.S. 145 f. 58	left center	*Asplenium platyneuron* (L.) B.S.P	Aspleniaceae
H.S. 145 f. 58	bottom left	*Symphyotrichum dumosum* (L.) Nesom	Asteraceae
H.S. 145 f. 58	bottom next to left	*Silene virginica* L.	Caryophyllaceae
H.S. 145 f. 58	top three	*Monarda punctata* L. var. *punctata*	Lamiaceae
H.S. 145 f. 58	bottom right	*Platanthera ciliaris* (L.) Lindley	Orchidaceae
H.S. 145 f. 58	bottom second from right	*Dichanthelium boscii* (Poiret) Gould & Clark	Poaceae
H.S. 145 f. 58	bottom center fern	*Pleopeltis polypodioides* (L.) E.G. Andrews & Windham subsp. *michauxiana* (Weatherby) E.G. Andrews & Windham	Polypodiaceae
H.S. 145 f. 59	bottom left	*Yucca filamentosa* L.	Agavaceae
H.S. 145 f. 59	bottom right	*Solidago odora* Ait. (with gall)	Asteraceae
H.S. 145 f. 59	top center	*Oxydendrum arboreum* (L.) D.C.	Ericaceae
H.S. 145 f. 59	top right	*Vaccinium arboreum* Marsh.	Ericaceae
H.S. 145 f. 59	right center	*Castanea pumila* (L.) P. Mill.	Fagaceae
H.S. 145 f. 59	top left	*Maianthemum racemosum* (L.) Link subsp. *racemosum*	Ruscaceae
H.S. 145 f. 59	bottom center	*Vitis aestivalis* Michx.	Vitaceae
H.S. 145 f. 60	top left	*Verbesina walteri* Shinners	Asteraceae
H.S. 145 f. 60	bottom right	*Clethra alnifolia* L.	Clethraceae
H.S. 145 f. 60	center right	*Clitoria mariana* L. var. *mariana*	Fabaceae
H.S. 145 f. 60	bottom	*Rosa palustris* Marsh.	Rosaceae
H.S. 145 f. 60	second from left bottom	*Polygonatum biflorum* (Walt.) Ell.	Ruscaceae
H.S. 145 f. 60	top center two	*Salix humilis* Marsh.	Salicaceae
H.S. 145 f. 60	bottom left	*Smilax rotundifolia* L.	Smilacaceae
H.S. 145 f. 60	center left	*Vitis rotundifolia* Michx.	Vitaceae
H.S. 145 f. 61	center right	*Eupatorium* sp.	Asteraceae
H.S. 145 f. 61	top center	*Clethra alnifolia* L.	Clethraceae
H.S. 145 f. 61	bottom left	*Cyrilla racemiflora* L.	Cyrillaceae
H.S. 145 f. 61	top right	*Cephalanthus occidentalis* L.	Rubiaceae
H.S. 145 f. 61	bottom center	*Cephalanthus occidentalis* L.	Rubiaceae
H.S. 145 f. 61	top left	*Phegopteris hexagonoptera* (Michx.) Fée	Thelypteridaceae
H.S. 145 f. 62	bottom left	*Asclepias tuberosa* L.	Apocynaceae
H.S. 145 f. 62	bottom right	*Cirsium* sp.	Asteraceae
H.S. 145 f. 62	top right	*Ipomoea pandurata* (L.) G.F.W. Meyer	Convolvulaceae
H.S. 145 f. 62	top left	*Sabatia angularis* (L.) Pursh	Gentianaceae
H.S. 145 f. 62	top center	*Rumex crispus* L.	Polygonaceae
H.S. 145 f. 63	bottom right	Indet.	
H.S. 145 f. 63	bottom center, folded	*Helianthus heterophyllus* Nutt.	Asteraceae
H.S. 145 f. 63	bottom, skip helianthus in middle	*Lonicera sempervirens* L.	Caprifoliaceae

H.S. 145 f. 63	top left	*Commelina erecta* L.	Commelinaceae
H.S. 145 f. 63	top center	*Cephalanthus occidentalis* L.	Rubiaceae
H.S. 145 f. 64	right	*Oxydendrum arboreum* (L.) D.C.	Ericaceae
H.S. 145 f. 64	bottom center	*Chamaelirium luteum* (L.) A. Gray	Heloniadaceae
H.S. 145 f. 64	top left	*Cephalanthus occidentalis* L.	Rubiaceae
H.S. 145 f. 65	top second from right	Indet.	
H.S. 145 f. 65	bottom center	*Desmodium rotundifolium* D.C.	Fabaceae
H.S. 145 f. 65	bottom right	*Chamaelirium luteum* (L.) A. Gray	Heloniadaceae
H.S. 145 f. 65	top	*Magnolia tripetala* (L.) L.	Magnoliaceae
H.S. 145 f. 65	bottom left	*Ceanothus americanus* L.	Rhamnaceae
H.S. 145 f. 66	top left	*Prenanthes* sp.	Asteraceae
H.S. 145 f. 66	bottom left	*Oxydendrum arboretum* (L.) DC	Ericaceae
H.S. 145 f. 66	top center	*Sisyrinchium angustifolium* P. Mill.	Iridaceae
H.S. 145 f. 66	bottom right	*Pycnanthemum flexuosum* (Walt.) B.S.P.	Lamiaceae
H.S. 145 f. 66	top right	*Penstemon* sp.	Plantaginaceae
H.S. 145 f. 48	middle right	*Cypripedium parviflorum* Salisb. var. *pubescens* (Willd.) Knight	Orchidaceae
H.S. 158 f. 129	lower center and right	*Antennaria plantaginifolia* (L.) Richardson	Asteraceae
H.S. 158 f. 129	upper right	*Chrysopsis mariana* (L.) Ell.	Asteraceae
H.S. 158 f. 129	3 upper left	*Pterocaulon pycnostachyum* (Michx.) Ell.	Asteraceae
H.S. 158 f. 129	lower left	*Verbesina* (probably *V. virginica* L.)	Asteraceae
H.S. 158 f. 151	whole sheet	*Helianthus divaricatus* L.	Asteraceae
H.S. 158 f. 214		*Houstonia purpurea* L.	Rubiaceae
H.S. 159 f. 108	top	*Fagus grandifolia* Ehrh.	
H.S. 159 f. 108	bottom	*Ulmus americana* L.	
H.S. 159 f. 115	top	*Quercus elliottii* Wilbur	Fagaceae
H.S. 159 f. 115	bottom	*Quercus virginiana* P. Mill.	Fagaceae
H.S. 159 f. 117		*Carya tomentosa* (Lam. ex Poir.) Nuttall	Juglandaceae
H.S. 159 f. 121	top	*Quercus velutina* Lam.	
H.S. 159 f. 122	top	*Quercus falcata* Michx.	Fagaceae
H.S. 159 f. 122	bottom	*Quercus nigra* L.	Fagaceae
H.S. 159 f. 123	all	*Quercus muehlenbergii* Engelm.	Fagaceae
H.S. 159 f. 124		*Quercus lyrata* Walt.	Fagaceae
H.S. 159 f. 124	124v	*Quercus shumardii* Buckley	Fagaceae
H.S. 159 f. 129		*Salix nigra* Marsh.	Salicaceae
H.S. 159 f. 224	top	*Smilax smallii* Morong	Smilacaceae
H.S. 242 f. 110	Bottom left under label	Indet.	Indet.
H.S. 242 f. 110	top right	*Carya tomentosa* (Lam. ex Poir.) Nutt. (leaflet)	Juglandaceae
H.S. 242 f. 110	top left	*Magnolia acuminata* L.	Magnoliaceae
H.S. 242 f. 110	bottom left and right	*Nyssa biflora* Walt.	Nyssaceae
H.S. 242 f. 111	right center	moss	

H.S. 242 f. 111	bottom	*Asimina triloba* (L.) Dunal	Annonaceae
H.S. 242 f. 111	top center	Fabaceae sp.	Fabaceae
H.S. 242 f. 111	top left	*Galium hispidulum* Michx.	Rubiaceae
H.S. 242 f. 113		*Smilax laurifolia* L.	Smilacaceae
H.S. 242 f. 114	bottom left	Indet.	
H.S. 242 f. 114	top left	*Ludwigia palustris* (L.) Ell.	Onagraceae
H.S. 242 f. 114	bottom center	*Arundinaria tecta* (Walt.) Muhl.	Poaceae
H.S. 242 f. 115	Stenanthium densum	*Stenanthium densum* (Desrouss.) Zomlefer & Judd	Melanthiaceae
H.S. 242 f. 115	left	*Houstonia purpurea* L.	Rubiaceae
H.S. 242 f. 115	top center	*Physalis* sp.	Solanaceae
H.S. 242 f. 116	far left	*Hypericum virginicum* L.	Hypericaceae
H.S. 242 f. 116	center	*Oxalis dillenii* Jacq.	Oxalidaceae
H.S. 242 f. 116	bottom right	*Dichanthelium commutatum* (Schultes) Gould	Poaceae
H.S. 242 f. 117	bottom left	*Elephantopus tomentosus* L.	Asteraceae
H.S. 242 f. 117	bottom right	*Carex louisianica* L.H. Bailey	Cyperaceae
H.S. 242 f. 117	top center (male flower), female flower below	*Chamaelirium luteum* (L.) A. Gray	Heloniadaceae
H.S. 242 f. 117	top left	*Lilium michauxii* Poir.	Liliaceae
H.S. 242 f. 117	bottom center	*Potentilla norvegica* L.	Rosaceae
H.S. 242 f. 118a	bottom left (two	Indet	
H.S. 242 f. 118a	bottom	*Elephantopus tomentosus* L. (goes with specimen on previous page)	Asteraceae
H.S. 242 f. 118a	top left	*Quercus nigra* L.	Fagaceae
H.S. 242 f. 118a	bottom center right	*Sisyrinchium atlanticum* E.P. Bickn.	Iridaceae
H.S. 242 f. 118a	top right	*Vulpia octoflora* (Walt.) Rydb.	Poaceae
H.S. 242 f. 118a	bottom right	*Rumex hastatulus* Baldwin	Polygonaceae
H.S. 242 f. 118b	top left	*Juniperus virginiana* L.	Cupressaceae
H.S. 242 f. 118b	big one	*Quercus velutina* Lam.	Fagaceae
H.S. 242 f. 118b	top right, bottom left	*Quercus falcata* Michx.	Fagaceae
H.S. 242 f. 119	all	*Quercus phellos* L.	Fagaceae
H.S. 242 f. 120		*Carya tomentosa* (Lam. ex Poir.) Nutt.	Juglandaceae
H.S. 242 f. 121		*Carya tomentosa* (Lam. ex Poir.) Nutt.	Juglandaceae
H.S. 242 f. 122	top	*Ilex opaca* Ait.	Aquifoliaceae
H.S. 242 f. 122	bottom	*Salix nigra* Marsh.	Salicaceae
H.S. 242 f. 123		*Cornus florida* L.	Cornaceae
H.S. 242 f. 123	top right	*Nyssa biflora* Walt.	Cornaceae
H.S. 242 f. 124		*Prunus serotina* Ehrh.	Rosaceae
H.S. 242 f. 125		*Cornus foemina* Mill. (= *Cornus*	Cornaceae

		asperifolia Michx. per Weakley)	
H.S. 242 f. 126	upper right	*Osmanthus americanus* (L.) Benth & Hook. f. ex A. Gray = *Cartrema americana* (L.) Nesom	Oleaceae
H.S. 242 f. 126		*Prunus caroliniana* (P. Mill.) Ait.	Rosaceae
H.S. 242 f. 127	Bottom Middle	Indet.	
H.S. 242 f. 127	Bottom Left	*Gayhussacta frondosa* (L.) Torrey & A. Gray ex Torrey	Ericaceae
H.S. 242 f. 127	top right	*Lyonia mariana* (L.) D. Don	Ericaceae
H.S. 242 f. 127	Top Middle	*Vaccinium tenellum* Ait.	Ericaceae
H.S. 242 f. 127	top left	*Crataegus* sp.	Rosaceae
H.S. 242 f. 127	Middle Right and leaf at Bottom Right	*Symplocos tinctoria* (L.) L'Her.	Symplocaceae
H.S. 242 f. 128		*Vaccinium stamineum* L.	Ericaceae
H.S. 242 f. 129	top left	*Ilex glabra* (L.) A. Gray	Aquifoliaceae
H.S. 242 f. 129	all	*Cercis canadensis* L.	
H.S. 242 f. 129	bottom right	*Robinia pseudoacacia* L.	Fabaceae
H.S. 242 f. 130	right	*Itea virginica* L.	Iteaceae
H.S. 242 f. 130	left	*Prunus caroliniana* (P. Mill.) Ait.	Rosaceae
H.S. 242 f. 131	bottom left	Indet.	
H.S. 242 f. 131	large branch	*Lyonia lucida* (Lam.) K. Koch	Ericaceae
H.S. 242 f. 132	top right	*Rhododendron viscosum* (L.) Torrey	Ericaceae
H.S. 242 f. 132	top left (leaf)	*Magnolia virginiana* L.	Magnoliaceae
H.S. 242 f. 132	bottom right (leaf)	*Magnolia virginiana* L.	Magnoliaceae
H.S. 242 f. 132	bottom left	*Acer rubrum* L.	Sapindaceae
H.S. 242 f. 133	bottom	Indet.	
H.S. 242 f. 133	top right	*Rhododendron canescens* (Michx.) Sweet	Ericaceae
H.S. 242 f. 133	top left	*Magnolia virginiana* L.	Magnoliaceae
H.S. 242 f. 134		*Magnolia virginiana* L.	Magnoliaceae
H.S. 242 f. 135	Middle Left and Top Left	*Gelsemium sempervirens* (L.) St. Hil.	Gelsemiaceae
H.S. 242 f. 135	bottom right (seedling)	*Liriodendron tulipifera* L.	Magnoliaceae
H.S. 242 f. 135	middle	*Smilax smallii* Morong	Smilacaceae
H.S. 242 f. 136	most	*Apocynum cannabinum* L.	Apocynaceae
H.S. 242 f. 136	bottom right	*Quercus michauxii* Nutt.	Fagaceae
H.S. 242 f. 129	top right	*Ilex glabra* (L.) A. Gray	Aquifoliaceae

TAXA BY FAMILY

Pteridophytes

Aspleniaceae	*Asplenium platyneuron* (L.) B.S.P.	H.S. 145 f. 58
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn	H.S. 145 f. 48
Polypodiaceae	*Pleopeltis polypodioides* (L.) E.G. Andrews & Windham subsp. *michauxiana* (Weatherby) E.G. Andrews & Windham	H.S. 145 f. 47, H.S. 145 f. 58
Thelypteridaceae	*Phegopteris hexagonoptera* (Michx.) Fée	H.S. 145 f. 61

Basal Angiosperms

Annonaceae	*Asimina triloba* (L.) Dunal	H.S. 242 f. 111
Magnoliaceae	*Magnolia tripetala* (L.) L.	H.S. 145 f. 57, H.S. 145 f. 65
Magnoliaceae	*Magnolia acuminata* L.	H.S. 242 f. 110
Magnoliaceae	*Magnolia virginiana* L.	H.S. 242 f. 132, H.S. 242 f. 133, H.S. 242 f. 134
Magnoliaceae	*Liriodendron tulipifera* L.	H.S. 242 f. 135

Gymnosperms

Cupressaceae	*Taxodium distichum* (L.) L.C. Richard	H.S. 145 f. 50
Cupressaceae	*Juniperus virginiana* L.	H.S. 242 f. 118

Monocots

Bromeliaceae	*Tillandsia usneoides* (L.) L.	H.S. 145 f. 51
Commelinaceae	*Commelina erecta* L.	H.S. 145 f. 63
Cyperaceae	*Cyperus echinatus* (L.) Wood	H.S. 145 f. 45
Cyperaceae	*Cyperus* sp.	H.S. 145 f. 46
Cyperaceae	*Scirpus cyperinus* (L.) Kunth	H.S. 145 f. 51, H.S. 145 f. 52
Cyperaceae	*Carex louisianica* L.H. Bailey	H.S. 242 f. 117
Heloniadaceae	*Chamaelirium luteum* (L.) A. Gray	H.S. 145 f. 64, H.S. 145 f. 65, H.S. 242 f. 117
Iridaceae	*Sisyrinchium angustifolium* P. Mill.	H.S. 145 f. 66
Iridaceae	*Sisyrinchium atlanticum* E.P. Bickn.	H.S. 242 f. 118
Liliaceae	*Lilium michauxii* Poir.	H.S. 145 f. 55, H.S. 242 f. 117
Lilliaceae	*Lilium superbum* L.	H.S. 145 f. 47
Melanthiaceae	*Stenanthium densum* (Desrouss.) Zomlefer & Judd	H.S. 242 f. 115

Orchidaceae	*Cypripedium parviflorum* Salisb. var. *pubescens* (Willd.) Knight	H.S. 145 f. 48
Orchidaceae	*Cypripedium parviflorum* Salisb. var. *pubescens* (Willd.) Knight	H.S. 145 f. 50
Orchidaceae	*Hexalectris spicata* (Walt.) Barnhart	H.S. 145 f. 50
Orchidaceae	*Platanthera ciliaris* (L.) Lindley	H.S. 145 f. 47, H.S. 145 f. 58
Poaceae	Poaceae sp.	H.S. 145 f. 52, H.S. 145 f. 53
Poaceae	*Arundinaria tecta* (Walt.) Muhl.	H.S. 242 f. 114
Poaceae	*Chasmanthium sessiflorum* (Poir.) Yates	H.S. 145 f. 54
Poaceae	*Dichanthelium boscii* (Poir.) Gould & Clark	H.S. 145 f. 58
Poaceae	*Dichanthelium commutatum* (Schultes) Gould	H.S. 242 f. 116
Poaceae	*Vulpia octoflora* (Walt.) Rydb.	H.S. 242 f. 118a
Poaceae	*Zizania aquatica* L. var. *aquatica*	H.S. 145 f. 53
Ruscaceae	*Mananthemum racemosum* (L.) Link	H.S. 145 f. 50, H.S. 145 f. 59
Ruscaceae	*Polygonatum biflorum* (Walt.) Ell.	H.S. 145 f. 60
Smilacaceae	*Smilax rotundifolia* L.	H.S. 145 f. 60
Smilacaceae	*Smilax laurifolia* L.	H.S. 242 f. 113
Smilacaceae	*Smilax smallii* Morong	H.S. 159 f. 224, H.S. 242 f. 135

Eudicots

Acanthaceae	*Ruellia caroliniensis* (J.F. Gmel.) Steud.	H.S. 145 f. 49
Adoxaceae	*Sambucus canadensis* L.	H.S. 145 f. 49
Agavaceae	*Yucca filamentosa* L.	H.S. 145 f. 59
Apocynaceae	*Asclepias tuberosa* L.	H.S. 145 f. 62
Apocynaceae	*Apocynum cannabinum* L.	H.S. 242 f. 136
Aquifoliaceae	*Ilex opaca* Ait.	H.S. 242 f. 122
Aquifoliaceae	*Ilex glabra* (L.) A. Gray	H.S. 242 f. 129
Asteraceae	*Ageratina altissima* King & H. Rob. var. *altissima*	H.S. 145 f. 54
Asteraceae	*Antennaria plantaginifolia* (L.) Richardson	H.S. 158 f. 129
Asteraceae	*Chrysopsis mariana* (L.) Ell.	H.S. 145 f. 49, H.S. 158 f. 129
Asteraceae	*Cirsium* sp.	H.S. 145 f. 62
Asteraceae	*Coreopsis tripteris* L.	H.S. 145 f. 45

Asteraceae	*Elephantopus tomentosus* L.	H.S. 242 f. 117, H.S. 242 f. 118a
Asteraceae	*Eupatorium* sp.	H.S. 145 f. 61
Asteraceae	*Eutrochium dubium* (Willd. ex Poir.) E.E. Lamont (= *Eupatoriadelphus dubius*)	H.S. 145 f. 50, H.S. 145 f. 51
Asteraceae	*Helianthus divaricatus* L.	H.S. 145 f. 45, H.S. 158 f. 151
Asteraceae	*Helianthus heterophyllus* Nutt.	H.S. 145 f. 63
Asteraceae	*Hieracium* sp.	H.S. 145 f. 48
Asteraceae	*Liatris squarrosa* (L.) Michx.	H.S. 145 f. 45, H.S. 145 f. 52
Asteraceae	*Prenanthes* sp.	H.S. 145 f. 66
Asteraceae	*Pterocaulon pycnostachyum* (Michx.) Ell.	H.S. 158 f. 129
Asteraceae	*Solidago odora* Ait.	H.S. 145 f. 59
Asteraceae	*Symphyotrichum* sp.	H.S. 145 f. 48
Asteraceae	*Symphyotrichum dumosum* (L.) Nesom	H.S. 145 f. 58
Asteraceae	*Verbesina* (*Verbesina virginica* L.?)	H.S. 158 f. 129
Asteraceae	*Verbesina walteri* Shinners	H.S. 145 f. 60
Asteraceae	*Vernonia acaulis* (Walt.) Gleason	H.S. 145 f. 53
Bignoniaceae	*Bignonia capreolata* L.	H.S. 159 f. 224
Boraginaceae	*Onosmodium virginianum* (L.) A.DC (=*Lithospermum virginianum* L.)	H.S. 145 f. 46
Caprifoliaceae	*Lonicera sempervirens* L.	H.S. 145 f. 63
Caryophyllaceae	*Silene virginica* L.	H.S. 145 f. 58
Clethraceae	*Clethra alnifolia* L.	H.S. 145 f. 60, H.S. 145 f. 61
Convolvulaceae	*Ipomoea pandurata* (L.) G.F.W. Meyer	H.S. 145 f. 62
Cornaceae	*Cornus florida* L.	H.S. 242 f. 123
Cornaceae	*Cornus foemina* Mill. (= *Cornus asperifolia* Michx. per Weakley)	H.S. 242 f. 125
Cornaceae	*Nyssa biflora* Walt.	H.S. 242 f. 123
Cyrillaceae	*Cyrilla racemiflora* L.	H.S. 145 f. 49, H.S. 145 f. 50, H.S. 145 f. 61
Ericaceae	*Gaylussacia frondosa* (L.) Torrey & A. Gray ex Torrey	H.S. 242 f. 127
Ericaceae	*Lyonia lucida* (Lam.) K. Koch	H.S. 242 f. 131
Ericaceae	*Lyonia mariana* (L.) D. Don	H.S. 145 f. 47, H.S. 242 f. 127

Ericaceae	*Oxydendrum arboreum* (L.) DC	H.S. 145 f. 59, H.S. 145 f. 64, H.S. 145 f. 66
Ericaceae	*Rhododendron canescens* (Michx.) Sweet	H.S. 242 f. 133
Ericaceae	*Rhododendron viscosum* (L.) Torrey	H.S. 242 f. 132
Ericaceae	*Vaccinium arboreum* Marsh.	H.S. 145 f. 59
Ericaceae	*Vaccinium formosum* H.S. Andrews	H.S. 145 f. 48
Ericaceae	*Vaccinium tenellum* Ait.	H.S. 242 f. 127
Ericaceae	*Vaccinium stamineum* L.	H.S. 242 f. 128
Euphorbiaceae	*Euphorbia pubentissima* Michx.	H.S. 145 f. 45
Fabaceae	*Amphicarpaea bracteata* (L.) Fernald	H.S. 145 f. 49
Fabaceae	*Apios americana* Medik.	H.S. 145 f. 55, H.S. 145 f. 56
Fabaceae	*Cercis canadensis* L.	H.S. 242 f. 129
Fabaceae	*Chamaecrista fasciculata* (Michx.) Greene	H.S. 145 f. 46
Fabaceae	*Clitoria mariana* L.	H.S. 145 f. 48
Fabaceae	*Clitoria mariana* L. var. *mariana*	H.S. 145 f. 60
Fabaceae	*Desmodium paniculatum* (L.) DC	H.S. 145 f. 50
Fabaceae	*Desmodium rotundifolium* D.C.	H.S. 145 f. 65
Fabaceae	*Desmodium tenuifolium* Torrey & A. Gray	H.S. 145 f. 45
Fabaceae	Fabaceae sp.	H.S. 242 f. 111
Fabaceae	*Galactia regularis* (L.) B.S.P.	H.S. 145 f. 45
Fabaceae	*Hylodesmum nudiflorum* (L.) H. Ohashi & R.R. Mill (= *Desmodium nudiflorum* (L.) DC)	H.S. 145 f. 49
Fabaceae	*Robinia pseudoacacia* L.	H.S. 242 f. 129
Fabaceae	*Rhynchosia difformis* (Ell.) D.C.	H.S. 145 f. 46
Fabaceae	*Rhynchosia tomentosa* (L.) Hook. & Arn.	H.S. 145 f. 46
Fabaceae	*Tephrosia spicata* (Walt.) Torrey & A. Gray	H.S. 145 f. 48
Fagaceae	*Castanea pumila* (L.) P. Mill.	H.S. 145 f. 59
Fagaceae	*Fagus grandifolia* Ehrh.	H.S. 159 f. 108
Fagaceae	*Quercus elliottii* Wilbur	H.S. 159 f. 115
Fagaceae	*Quercus falcata* Michx.	H.S. 159 f. 122, H.S. 242 f. 118b

Fagaceae	*Quercus lyrata* Walt.	H.S. 159 f. 124
Fagaceae	*Quercus michauxii* Nutt.	H.S. 242 f. 136
Fagaceae	*Quercus muehlenbergii* Engelm.	H.S. 159 f. 123
Fagaceae	*Quercus nigra* L.	H.S. 159 f. 122, H.S. 242 f. 118a
Fagaceae	*Quercus pagoda* Raf.	H.S. 159 f. 125
Fagaceae	*Quercus phellos* L.	H.S. 242 f. 119
Fagaceae	*Quercus shumardii* Buckley	H.S. 159 f. 124
Fagaceae	*Quercus velutina* Lam.	H.S. 159 f. 121, H.S. 242 f. 118b
Fagaceae	*Quercus virginiana* P. Mill.	H.S. 159 f. 115
Gelsemiaceae	*Gelsemium sempervirens* (L.) St. Hil.	H.S. 242 f. 135
Gentianaceae	*Sabatia angularis* (L.) Pursh	H.S. 145 f. 62
Gentianaceae	*Sabatia* sp. (*Sabatia campanulata* (L.) Torrey?)	H.S. 145 f. 48
Hypericaceae	*Hypericum virginicum* L.	H.S. 242 f. 116
Iteaceae	*Itea virginica* L.	H.S. 242 f. 130
Juglandaceae	*Carya tomentosa* (Lam. ex Poir.) Nutt. (leaflet)	H.S. 159 f. 117, H.S. 242 f. 110, H.S. 242 f. 120, H.S. 242 f. 121
Lamiaceae	*Monarda punctata* L. var. *punctata*	H.S. 145 f. 58
Lamiaceae	*Pycnanthemum flexuosum* (Walt.) B.S.P.	H.S. 145 f. 66
Lythraceae	*Decodon verticillatus* (L.) Ell.	H.S. 145 f. 52, H.S. 145 f. 54
Nyssaceae	*Nyssa biflora* Walt.	H.S. 242 f. 110
Nyssaceae	*Nyssa sylvatica* Marsh.	H.S. 145 f. 56
Oleaceae	*Osmanthus americanus* (L.) Benth & Hook. f. ex A. Gray = *Cartrema americana* (L.) Nesom	H.S. 242 f. 126
Onagraceae	*Oenothera fruticosa* L.	H.S. 145 f. 48
Onagraceae	*Ludwigia palustris* (L.) Ell.	H.S. 242 f. 114
Orobanchaceae	*Agalinis setacea* (J.F. Gmel.) Raf.	H.S. 145 f. 47
Orobanchaceae	*Aureolaria virginica* (L.) Penn.	H.S. 145 f. 49
Oxalidaceae	*Oxalis dillenii* Jacq.	H.S. 242 f. 116
Plantaginaceae	*Penstemon* sp.	H.S. 145 f. 49, H.S. 145 f. 66
Polygonaceae	*Rumex crispus* L.	H.S. 145 f. 62
Polygonaceae	*Rumex hastatulus* Baldwin	H.S. 242 f. 118a

Ranunculaceae	*Thalictrum thalictroides* (L.) Eames & Boivin	H.S. 145 f. 49
Rhamnaceae	*Ceanothus americanus* L.	H.S. 145 f. 65
Rosaceae	*Crataegus* sp.	H.S. 242 f. 127
Rosaceae	*Potentilla norvegica* L.	H.S. 242 f. 117
Rosaceae	*Prunus serotina* Ehrh.	H.S. 242 f. 124
Rosaceae	*Prunus carolmiana* (P. Mill.) Ait.	H.S. 242 f. 126, H.S. 242 f. 130
Rosaceae	*Rosa palustris* Marsh.	H.S. 145 f. 60
Rubiaceae	*Houstonia purpurea* L.	H.S. 158 f. 214
Rubiaceae	*Cephalanthus occidentalis* L.	H.S. 145 f. 61, H.S. 145 f. 63, H.S. 145 f. 64
Rubiaceae	*Galium hispidulum* Michx.	H.S. 242 f. 111
Rubiaceae	*Houstonia purpurea* L.	H.S. 242 f. 115
Salicaceae	*Salix humilis* Marsh.	H.S. 145 f. 60
Salicaceae	*Salix nigra* Marsh.	H.S. 242 f. 122, H.S. 159 f. 129
Sapindaceae	*Acer rubrum* L.	H.S. 242 f. 132
Solanaceae	*Physalis* sp.	H.S. 242 f. 115
Symplocaceae	*Symplocos tinctoria* (L.) L'Her.	H.S. 242 f. 127
Ulmaceae	*Ulmus americana* L.	H.S. 159 f. 108
Verbenaceae	*Verbena carnea* Medik.	H.S. 145 f. 47
Vitaceae	*Vitis aestivalis* Michx.	H.S. 145 f. 59
Vitaceae	*Vitis rotundifolia* Michx.	H.S. 145 f. 60

DISCUSSION

Like the other volumes in the Sloane Herbarium, the volumes containing Lawson's specimens contain numerous addenda in the form of handwritten notes and pasted-on labels. These were placed on the pages by Petiver and the subsequent three centuries of curators of the collection. Of most interest to us are the handwritten notes that Lawson sent Petiver along with his plant specimens. Many of these notes contain collection dates and locations. We have used these collection dates to organize the discussion, presenting specimens in more or less chronological order.

Some of these handwritten notes include page and line references to *A New Voyage*. Where possible, we have incorporated Lawson's notes and botanical observations as published in *A New Voyage* (A New Voyage 2014) into our own discussion for the insight they offer into Lawson's thoughts about his specimens and the natural world of colonial days. (We have taken all text from the version published online by the University of North Carolina's Documenting the American South project.)

We have attempted to transcribe Lawson's labels but find his handwriting quite challenging to decipher and so our attempts are incomplete and probably inaccurate. Our learning to read Lawson is very much a work in progress. We revisit these labels periodically in the hope of finding fresh

inspiration, which does occasionally happen; sometimes a previously indecipherable label comes into clear focus on the 9th or 10th viewing. We invite readers to visit the images and improve on our efforts!

We do not assume that physical proximity between a note and a specimen necessarily means the two are related, though in many cases they clearly are. Bellis pointed out that a number of specimens appear to have been mislabeled when the pages were prepared, perhaps by Petiver mixing up notes and specimens, though it is impossible to know where the errors crept in (Bellis 2009).

H.S. 145 – Spring 1710

H.S. 145 contains 66 folios, but the first 44 pages contain numerous mosses and plants collected by botanists other than Lawson in locations other than Virginia and North Carolina. Lawson's plants begin on f. 45. Lawson collected all of these plants in May and June of 1710. A number of them were collected on the Trent and Neuse Rivers; Bellis has include a useful map of Lawson's movements in his *Castanea* article (Bellis 2009).

There are a number of interesting specimens in this volume, enhanced by Lawson's handwritten notes. The *Hexalectris spicata* on H.S. 145 f. 50 might be the earliest collection of this species. On the top right of H.S. 145 f. 49 is a specimen of *Ruellia carolimensis* with a bit of *Amphicarpea bracteata* wrapped around the stem.

H.S. 145 f. 47 contains a somewhat deteriorated specimen of *Lilium superbum* at the top left. We identified on the basis of the spots on the corolla – an exercise in forensic botany with the tiny pieces left of this plant. We have identified the specimens on the bottom right and left of H.S. 145 f. 55 as *Lilium michauxii*, but the spots do not go far up the petal, so this could also be a very early collection of *Lilium pyrophilum*.

H.S. 145. f. 48, top left, contains a specimen of *Vaccinium formosum*, the southern highbush blueberry. Pasted over the stem is a handwritten note reading "The largest huckleberry see page 104 the last sect of these fruits these green berries on the stem were gotten in Norfolk County in Virginia May the 10th." Bellis identifies this as one of the first specimens Lawson collected, before he'd even left Norfolk (Bellis 2009). Another "winter huckle berry" appears on the top right of H.S. 145 f. 59: sparkleberry, *Vaccinium arboreum*.

Page 104 of Lawson's *A New Voyage* tells us about huckleberries:

"Hurts.

The Hurts, Huckle-Berries, or Blues of this Country, are four sorts, which we are well acquainted withal; but more Species of this sort, and all others, Time and Enquiry must discover. The first sort is the same Blue or Bilberry, that grows plentifully in the North of England, and in other Places, commonly on your Heaths, Commons, and Woods, where Brakes or Fern grows.

The second sort grows on a small Bush in our Savannas and Meads, and in the Woods. They are larger than the common Fruit, and have larger Seed.

The third grows on the single Stem of a Stick that grows in low good Land, and on the Banks of Rivers. They grow three or four Foot high, and are very pleasant like the first sort, but larger.

The fourth sort grows upon Trees, some ten and twelve Foot high, and the Thickness of a Man's Arm; these are found in the Runs and low Grounds, and are very pleasant, and bear wonderfully. The English sometimes dry them in the Sun, and keep them to use in the Winter,

instead of Currants. The Indians get many Bushels, and dry them on Mats, whereof they make Plum-Bread, and many other Eatables. They are good in Tarts, or infused in Liquors."

Zizania aquatica var. *aquatica*, H.S. 145 f. 53, was an important food grain for native Americans. Weakley notes that it is now uncommon in North Carolina. Lawson did not, however, remark on Indians using this grain for food. On pp. 75-76 of *A New Voyage* he discusses rice, but certainly he means *Oryza sativa*, which was brought into cultivation in the Carolinas in the 1690s: "There are several sorts of Rice, some bearded, others not, besides the red and white; But the white Rice is the best. Yet there is a sort of perfum'd Rice in the East-Indies, which gives a curious Flavour, in the Dressing. And with this sort America is not yet acquainted; neither can I learn, that any of it has been brought over to Europe; the Rice of Carolina being esteem'd the best that comes to that Quarter of the World. It is of great Increase, yielding from eight hundred to a thousand-fold, and thrives best in wild Land, that has never been broken up before."

On H.S. 145 f. 59, top center, is a specimen of *Oxydendrum arboreum*, also known as sourwood or sorrel-tree. Lawson sent it to Petiver with a note reading "Sourwood tree pag 98 ??? ?? Gott in Trent River June 16th 1710." On page 98 of *A New History*, he writes "The Sorrel, or Sowr-Wood-Tree, is so call'd, because the Leaves taste like Sorrel. Some are about a Foot or ten Inches Diameter. I am unacquainted with its Vertues at present."

Another specimen of sourwood appears on H.S. 145 f. 64 with the note "Sourwood vid before" and a penciled notation to "see 59," referring to the previous specimen of *Oxydendrum*. This penciled notation is one of many that were added to the pages of the Sloane collections in the early 20th century by James Britten, an assistant in the Department of Botany at the NHM (Bellis 2009).

H.S. 145 f. 60 contains several of Lawson's handwritten labels on specimens collected in May and June of 1710. The top center specimen is *Salix humilis*, which he described as "a species of willow gotten on the sand banks near Ranoak ... May the 29th 1710." He declares the specimen of *Verbesina walteri* on the top left of the page as "Unknown," and notes that he collected it on the Trent River on June 13, 1710. The *Clitoria mariana* var. *mariana* he describes as "A sort of vetch gotten in Trent River June 19th 1710." On June 20 Lawson collected a *Polygonatum biflorum* at the Neus River, but wrote that it was "a plant unknown to me."

H.S. 145 f. 61 contains two specimens of *Cephalanthus occidentalis*. The bottom one bears the label "Chinkapin in flower Jun the ?? 1710 Trent River pag 99." Of course, the herbarium specimens are not chestnuts of any sort; perhaps Lawson confused the flowers after he took the cuttings? In any case, on p. 99 of *A New Voyage*, Lawson writes, "Chinkapin is a sort of Chesnut, whose Nuts are most commonly very plentiful; insomuch that the Hogs get fat with them. They are rounder and smaller than a Chesnut, but much sweeter. The Wood is much of the Nature of Chesnut, having a Leaf and Grain almost like it. It is used to timber Boats, Shallops, &c. and makes any thing that is to endure the Weather. This and the Hiccory are very tough Rods used to whip Horses withal; yet their Wood, in Substance, is very brittle. This Tree the Vine much delights to twist about. It's good Fire-Wood, but very sparkling, as well as Sassafras."

On June 4, 1710, Lawson collected a specimen of *Chamaelirium luteum* (H.S. 145 f. 65). His label reads "The celebrated snake root Trent River June 4th 1710." Whether or not this species is actually useful against snakebite, blazing stars are traditional herbal medicines. (See, eg Crellin and Bass 1990). Another *Chamaelirium luteum* appears on H.S. 242 f. 117, labeled as "A bulbous sort of a Lilly common here in March & April." This page also contains a label reading "The celebrated snake root." Its placement between the *Elephantopus tomentosus* on the bottom left of - or the *Lilium michauxii* above it is somewhat confusing, but based on Lawson's previous collection of

Chamaelirium we imagine that is the snakeroot in question. Lawson mentions snakeroots on p. 78 of *A New Voyage*, but this is not of much help with the herbarium specimens.

Also on June 4, Lawson collected a *Desmodium rotundifolium* and a *Ceanothus americanus* (both also H.S. 145 f. 65) and a *Penstemon* (H.S. 145 f. 66) which he labeled a "Golden Rod," also from the Trent River area. The *Ceanothus* specimen bears an intriguing note that we have not yet deciphered satisfactorily; it appears to refer to a "red root flower and leaf" and to suggest that "This flower the ??? (Indians?) eat; the root cures sore mouths."

On H.S. 145 f. 62 is a specimen that we have identified as *Rumex crispus*, curly dock. Lawson's label reads "Wild Dock a sorrel Trent River June 20th 1710 vid with seed[?]". If this is indeed *Rumex crispus*, it is a Eurasian plant. *R. crispus* is a perennial weed today in North Carolina ("NC State TurfFiles" 2014); if it was already growing wild when Lawson explored the Trent River, it must have gained a foothold in the colonies almost as soon as the first Europeans set foot on Carolina shores. Lawson mentions dock, sorrel, and several other salad greens that grew from European seed on p. 77 of *A New Voyage*; the colonists had already found that their typical European crops grew well in Carolina.

The label on the specimen on the lower right of H.S. 145 f. 63 reads "Golden rod vid before 11." We cannot identify this specimen at all, but it does not appear to be in the genus *Solidago*. The bottom center specimen is a *Helianthus heterophyllus* that Lawson writes was collected at the Neuse River on June 29 1710.

Presumably at this point Lawson packed up this collection for shipment in July of 2010.

H.S. 242 – Winter 1710-Spring 1711

H.S. 242 contains specimens Lawson collected between December 1710 and May 1711. Dandy's description of the volume reads "Some plants gathered by Dr. Plukenet. Some plants gathered by Mr. Petiver. Alpine plants by Dr. Scheuchzer. Carolina plants by Mr. Lawson. Guinea plants from Mr. Staphorst. Garden at the Cape and other plants by Mr. Cunningham. Varieties of absynthium marinum by Dr. Blair. On the title-page is a list of 'Lawson's Virginia trees' in Petiver's hand." Dandy also includes a synopsis of contributors in addition to Plukenet and Petiver, in which Lawson's collections are listed as occurring on ff. 110-136 (Dandy 1958).

On the bottom left of H.S. 242 f. 110 is a mystery: a tiny specimen of something that appears to have trifoliate leaves — maybe a *Desmodium*, though really we have no idea — with a label pasted directly on top of it. This label is intriguing. We believe it reads something like this: "Jan. 29th 1711. Spontaneous trefoil of Carolina growing on the fork of Neus River and in other places, having shed from flower like drops of blood a sweet herbage ??? all spontaneous trefoils are more hairy here than in England." Too bad the specimen is almost completely obscured!

Two evergreens collected in early 1711 appear on H.S. 242 f. 126. On January 31, 1711, Lawson collected an "evergreen" resembling a holly at "Mr. Hancock's on the south side Neus R." This specimen appears to be an *Osmanthus americanus* (currently identified by Weakley as *Cartrema americana*. The rest of the page contains specimens of "the pleasantest evergreen," *Prunus carolinana*, collected on February 8, 1711. Both of these specimens are accompanied by very descriptive labels.

Lawson collected a moss that appears on the upper right of H.S. 242 f. 111, which he describes as "moss on little soft boggy hillocks, Feb. ?th 1711 on the side Neus." The same page contains a specimen of *Asimina triloba* with a label reading "Pawpaw I think April 30." It also

contains a specimen of *Galium hispidulum* with a note reading: "Feb. 8th 1711, having black berries thereon as big as pepper corns now ripe a fecundant growing in most light fertile lands." Is "fecundant" a term for a weed?

H.S. 242 f. 122 contains a specimen of *Ilex opaca* with a note presenting "2 forks of holly these leaves being more prickly and regular than what you have before; gotten at broad Creeks mouth on the north side Neus Feb. 8th 1711."

H.S. 242 f. 113 contains a specimen of *Smilax laurifolia*. This specimen contains two notes. One, pasted over the stem, reads "An evergreen vine gotten at Carolina Feb. 20th 1711 having green unripe berries thereon." The other, stuck on the top of the page almost as an afterthought, reads "Evergreen vine with fruit ripe in Jan."

On the top of H.S. 242 f. 114 is a specimen of *Ludwigia palustris*. Its label reads "Growing on a sandy beach on the north side Neus cliff near Green landing Feb. 18 1711." An *Arundinaria tecta* on this page is described as a "Small reed growing in the low soft grounds of Neus and other places Feb. 9th 1711."

Several specimens of *Prunus serotina* appear on H.S. 242 f. 124, one bearing the note: "Native black cherry pag. 104 line ??, gotten in Little ?? April 12 1711." In *A New Voyage*, Lawson writes, "The Cherries of the Woods grow to be very large Trees. One sort, which is rarely found, is red, and not much unlike the Cornel-Berry. But the common Cherry grows high, and in Bunches, like English Currants, but much larger. They are of a bitterish sweet Relish, and are equally valuable with our small Black-Cherries, for an Infusion in Spirits. They yield a crimson Liquor, and are great Bearers."

On H.S. 242 f. 123 are several specimens of *Cornus florida* with a label reading "April 15th 1711 Dogwood pag 94...." Page 94 of *A New Voyage* states: "Dog-Wood is plentiful on our light Land, inclining to a rich Soil. It flowers the first in the Woods; its white Blossom making the Forest very beautiful. It has a fine Grain, and serves for several Uses within doors; but is not durable. The Bark of this Root infused, is held an infallible Remedy against the Worms."

On April 19, 1711, Lawson collected a Maple, in this case *Acer rubrum* (H.S. 242 f. 132). Lawson uncharacteristically has little to say about the maple, which appears on p. 99 of *A New Voyage*: "The Maple, of which we have two sorts, is used to make Trenchers, Spinning-Wheels, &c withal."

Lawson collected a *Vaccinium tenellum* (H.S. 242 f. 127), which he identified as the "great seeded huckleberry," at Salmon Creek on April 20, 1711. He refers to p. 104 of *A New Voyage*, where he notes that the common sort of hurts or huckleberries are "the same Blue or Bilberry that grows plentifully in the North of England and in other Places, commonly on your Heaths, Commons, and Woods, where Brakes or Fern grows." The sort with the larger seed and fruit grows "on a small Bush in our Savannas and Meads, and in the Woods."

On the same page appears a *Crataegus*, which Law labels as a "Red Haw tree April 12, 1711." The red haw is of course a hawthorn, described on p. 107 of *A New Voyage*: "The Haw-thorn grows plentifully in some parts of this Country. The Haws are quite different from those in England, being four times as big, and of a very pleasant agreeable Taste. We make no use of this Plant, nor any other, for Hedges, because Timber is so plentiful at present. In my Judgment, the Honey-Locust would be the fittest for Hedges; because it is very apt to shoot forth many Sprouts and Succours from the Roots; besides, it is of a quick Growth; and very prickly."

Lawson collected a specimen of *Vulpia octoflora* (H.S. 242 f. 118a) on May 7th. (There are two consecutive pages with the number "118" handwritten in the upper right corner. We have designated the first one 118a and the second 118b.)

Lawson's specimen of *Carya tomentosa* on H.S. 242 f. 120 bears the note "Hicory May 7th 1711…." The same species appears on the next page with two notes, the top seeming to read "April 29? 1711 Salmon Creek." The two notes are difficult to decipher, but they appear to mention nuts and seeds, and the second concludes with the words "yet I take those two to be different." The first words may be "Smaller hicory with ??? and leaves may differ by a different ??? tree…"

On the upper right hand corner of H.S. 242 f. 123 is a specimen of *Nyssa biflora*. The note on this one "May 7th 1711 Col. Pollocks. I take this to be a Gum it grew under a very high bank by the water side." Lawson describes the black gums on p. 95 of *A New Voyage*: "Of the Black Gum there grows, with us, two sorts; both fit for Cart-Naves. The one bears a black, well-tasted Berry, which the Indians mix with their Pulse and Soups, it giving 'em a pretty Flavour, and scarlet Colour. The Bears crop these Trees for the Berries, which they mightily covet, yet kill'd in that Season, they eat very unsavory; which must be occasion'd by this Fruit, because, at other times, when they feed on Mast, Bears-Flesh is a very well-tasted Food. The other Gum bears a Berry in shape like the other, tho' bitter and ill-tasted. This Tree (the Indians report) is never wounded by Lightning. It has no certain Grain; and it is almost impossible to split or rive it."

A "Chestnut Oake" on H.S. 242 f. 136 is a *Quercus michauxii*. Of this tree, Lawson writes on p. 91: "Chesnut-Oak, is a very lofty Tree, clear of Boughs and Limbs, for fifty or 60 Foot. They bear sometimes four or five Foot through all clear Timber; and are the largest Oaks we have, yielding the fairest Plank. They grow chiefly in low Land, that is stiff and rich. I have seen of them so high, that a good Gun could not reach a Turkey, tho' loaded with Swan-Shot. They are call'd Chesnut, because of the Largeness and Sweetness of the Acorns."

H.S. 158 and H.S. 159 – Spring 1711

H.S. 158 and 159 are a pair of collections from diverse collectors enclosed in massive volumes. H.S. 158 contains 293 folios of small herbaceous plants, and H.S. 159 contains 400 folios of trees and shrubs. The specimens are systematically arranged and Petiver labeled most of them, some by hand and some with printed labels cut from his own publications.

It is difficult to determine who collected what in these volumes. Dandy observes that the names on the labels do not necessarily refer to collectors and that some labels bear the names of two collectors simultaneously. The specimens come from many different locations, including Newfoundland and Hudson Bay in addition to Virginia and Carolina. An "interesting series of North American oaks" appears on ff. 121-125.

Very few Lawson specimens appear in H.S. 158. Some specimens in H.S. 158 contain the notation "Virg. Marshall," suggesting that these were collected by James Marshall. Marshall was a surgeon who sent plants from Virginia to Petiver and Plukenet between 1695 and 1705 (Dandy 1958). For example, H.S. 158 f. 151 — which Dandy claims contains Lawson material — contains specimens of *Helianthus divaricatus* with the note "A sort of Snakeroot called St. Andrews Cross then length ??? of whose root always bends to the East. Lawson." Two of the specimens appear to have been collected by Marshall instead of Lawson.

H.S. 159 is a bit of a puzzle. It has enormous pages and numerous collections inside it. In the description of H.S. 159, Dandy writes that specimens from Lawson "are scattered throughout the volume," but he does not provide specific page numbers for Lawson specimens (Dandy 1958).
On the second page of H.S. 159 is a handwritten catalog, listing collectors and the pages on which their specimens appear. This list records Lawson's specimens on folios 114, 115, 122, and 224.

Confusingly, it lists Robert Ellis' specimens on folios 102-130, which overlaps with the Lawson specimens. Some specimens attributed to Mark Catesby also appear within that range. We have done our best to determine collectors based on the notes that appear on the specimens; anything with a note in Lawson's distinctive style and dates we have listed as collected by him.

For example, H.S. 159 f. 108 contains a specimen of *Fagus grandifolia* and a note reading "May 7th 1711. The Beech" in what appears to be Lawson's handwriting. Following these words is the word "Virginia" in what might be another hand. Below this is a specimen of *Ulmus* with a label in a different handwriting, stating that the plant was collected in Virginia in what appears to be 1711, on the York River.

H.S. 159 contains several of Lawson's oak specimens. At the bottom of H.S. 159 f. 115 is a specimen of *Quercus virginiana*, with the note: "The live oak which bears the sweet acorn pag line an evergreen these are two of this sort of evergreen oaks this bears an acorn sweet as a nut yielding a good eatable oyl; the other has an acorn and leaf much ??? and is bitter and of a yellow color so that nothing ??? to eat it which is quite contrary to their ????? of eating all they can meet with as soon as they see? what it is." It appears that Lawson left the page and line numbers blank, intending to add them later, perhaps after referring to his book. On page 92 of *A New Voyage* Lawson describes the acorns of live oaks as "sweet as chesnuts, and the Indians draw an oil from them, as sweet as that from the olive, tho' of an amber-colour."

A *Carya tomentosa* appears on H.S. 159 f. 117, bearing the note "April 20 1711 Salmon Creek. White hiccory of the large nuts the leaves smell like balm of Gilead."

Lawson describes three types of hickory in *A New Voyage*. Of the white hickory, he writes: "The Hiccory is of the Walnut-kind, and bears a Nut as they do, of which there are found three sorts. The first is that which we call the common white Hiccory. It is not a durable Wood; for if cut down, and exposed to the Weather, it will be quite rotten, and spoil'd in three Years; as will likewise the Beech of this Country. Hiccory Nuts have very hard Shells, but excellent sweet Kernels, with which, in a plentiful Year, the old Hogs, that can crack them, fatten themselves, and make excellent Pork. These Nuts are gotten, in great Quantities, by the Savages, and laid up for Stores, of which they make several Dishes and Banquets. One of these I cannot forbear mentioning; it is this: They take these Nuts, and break them very small betwixt two Stones, till the Shells and Kernels are indifferent small; And this Powder you are presented withal in their Cabins, in little wooden Dishes; the Kernel dissolves in your Mouth, and the Shell is spit out. This tastes as well as any Almond. Another Dish is the Soup which they make of these Nuts, beaten, and put into Venison-Broth, which dissolves the Nut, and thickens, whilst the Shell precipitates, and remains at the bottom. This Broth tastes very rich."

Lawson describes *Quercus nigra* (H.S. 159 f. 122) as an "Olive coloured water oak. May 10 1711. A beautiful water oak tho not an evergreen."

A specimen of *Quercus shumardii* appears on H.S. 159 f. 124; it is distinguishable from *Quercus rubra* by the tufts of hairs in the leaf axils. Of this tree, Lawson observes: "April 20th, 1711; a leaf of red oak got at Salmon Creek, pag. 92 line 3." In *A New Voyage*, Lawson writes "We have Red Oak, sometimes, in good Land, very large, and lofty. 'Tis a porous Wood, and used to rive into Rails for Fences. 'Tis not very durable; yet some use this, as well as the two former, for Pipe and Barrel-Staves. It makes good Clap boards."

Lawson mailed his last package of specimens to Petiver in July 1711. He died soon after.

Conclusion

Lawson seems to have been an extraordinarily talented and energetic man, likely to have published more and contributed more to the cataloging of the biota of the Americas, had he lived longer. His *A New Voyage* displays both attention to detail and empathy for human desires. His approach to natural history is refreshingly multi-faceted — descriptions of plants and animals include physical appearance, natural habits, and also culinary and practical uses. Modern authors rarely write travelogues that also discuss ecology, biology, anthropology, cookery, and construction. Lawson also has provided an interesting exploration of pre-Linnaean taxonomy — on page 126, we learn that Insects of Carolina include alligators, snakes, and lizards, though p. 129 contains a wonderful description of rattlesnakes.

This essay is a continuation of the project begun in the 17th century, gathering the data needed to catalog the world's organisms. The great thing about doing it online is that we can now have chronological perspective — John Lawson definitely wasn't looking at the Carolina we see today — and we can make connections rapidly. Lawson worked hard on his book and his collection. He never finished his natural history, but he's still in the conversation.

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PHYLOGENY OF *FRAXINUS* SECT. *MELIOIDES* (OLEACEAE): REVIEW AND AN ALTERNATIVE HYPOTHESIS

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ABSTRACT

Molecular-phylogenetic hypotheses for the species of *Fraxinus* sect. *Melioides* by Jeandroz (1997), Wallander (2008), and Hinsinger et al. (2013) are summarized and reviewed. There is disagreement among them and unexpected arrangements suggest that either misidentifications or speciation by hybridization, or both, may have affected the conclusions. An alternative phylogenetic hypothesis, subjectively developed mostly on the basis of morphology and geography, is presented here to summarize points of agreement and what seems plausible, perhaps to serve as a guide in further investigations. Sect *Melioides* is recognized here as comprising fifteen species divided informally among five groups: the Americana group (5 species), the Pennsylvanica group (7 species), and the Uhdei, Latifolia, and Papillosa groups (each with 1 species). Molecular data indicate that the American *F. cuspidata* and the Asian *F. platypoda*, *F. chinsanensis*, and *F. spaethiana* are closely related to sect. *Melioides* — these 4 species are regarded here as "aff. sect. *Melioides*," perhaps warranting separate formal recognition, since, if added to sect. *Melioides*, its morphological integrity is weakened.

Recent research by Hinsinger et al. (2013) is primarily concerned with patterns of diversification and geographic speciation in *Fraxinus* and provides interpretations of the geologic history of intercontinental dispersal and vicariance. They used "nuclear external transcribed spacers (nETS), phantastica gene sequences, and two chloroplast loci (trnH-psbA and rpl32-trnL) in combination with previously published and newly obtained nITS sequences to produce a time-calibrated multi-locus phylogeny of the genus." The phylogeny of *Fraxinus* also has been recently analyzed by Jeandroz et al. (1997, using nrITS) and by Wallander (2008, using nrITS). The Jeandroz study included 8 species of sect. *Melioides*, that of Wallander 10 species, that of Hinsinger et al. 9 species. Wallander and Hinsinger et al. included *F. cuspidata* of the western USA and three Asian species that molecular data indicate are closely related to sect. *Melioides*. None of the three studies appears to have included *F. smallii* (the tetraploid form of *F. americana*) or *F. pauciflora* — at least there were no samples identified as such.

Insofar as these three studies address broad patterns of diversification and biogeographic history and are relatively more reliant on identifications essentially at sectional level (rather than of individual species), results are plausible. But because of seeming anomalies in the relative phyletic positions of the sect. *Melioides* species, botanists interested in relationships among the North American *Fraxinus* species (which mostly are within sect. *Melioides*) probably will not be discouraged from further investigation. Hinsinger et al. (2013) suggested that apparent low differentiation at the genetic level among species of sect. *Melioides* (as interpreted from the poor phylogenetic resolution among samples) is a result of rapid radiation or recent gene exchange — explicitly eliminating misidentifications as a possible explanation (see below). Wallander (2008) noted that polyploidization and hybridization in sect. *Melioides* may be responsible for inconsistencies in the phylogenetic analysis; she also observed that "morphological and ecological variation" make identifications difficult.

Wallander (2008, p. 37) provided the following diagnostic description of sect. *Melioides*: "They are all medium-sized to large trees, deciduous and dioecious. The unisexual flowers are

apetalous and wind-pollinated. The female flowers consist of a calyx and one pistil, and the male flowers of two stamens with elongated anthers and a small calyx. There are no rudimental organs of the opposite sex in the flowers (a unique synapomorphy for this section). The calyx is persistent in the samaras, which have a distinctly terete seed cavity (except *Fraxinus caroliniana*). The wing may be decurrent along the seed cavity or not. In addition, the presence of flavones in the leaves (besides the plesiomorphic flavonols) is a synapomorphy for these species." While flavones are consistent feature of the the North American species, they also occur in *F. chiisanensis* (Chang et al. 2002), one of the species closely allied to sect. *Melioides* by molecular data, and Lee et al. (2012) found that they occur sporadically in Asian species of sect. *Ormus*.

Table 1. *Fraxinus* sect. *Melioides*

Sect. Melioides

Pennsylvanica Group
Fraxinus profunda
Fraxinus pennsylvanica
Fraxinus berlandieriana
Fraxinus velutina
Fraxinus coriacea
Fraxinus caroliniana
Fraxinus cubensis

Latifolia Group
Fraxinus latifolia

Papillosa Group
Fraxinus papillosa

Uhdei Group
Fraxinus uhdei

Americana Group
Fraxinus americana
Fraxinus albicans (syn: F. texensis)
Fraxinus smallii
Fraxinus biltmoreana
Fraxinus pauciflora

Aff. sect. Melioides

Asian Group
Fraxinus chiisanensis
Fraxinus platypoda
Fraxinus spaethiana

Cuspidata Group
Fraxinus cuspidata

In the taxonomic perspective here, *Fraxinus* sect. *Melioides* includes 15 North American species (Table 1). Molecular data indicate that (a) three species from southeast Asia and (b) one from the southwestern USA are most closely related to sect. *Melioides* — Hinsinger et al. explicitly included them as members of the section while Wallander mostly treated them as *incertae sedis* in her classification, as morphology places them outside of traditional sect. *Melioides*.

(a) In the Hinsinger et al. analysis *F. chiisanensis* (Korea), *F. platypoda* (China), and *F. spaethiana* (Japan) are members of the same clade and this small group is sister to North American sect. *Melioides* (Fig. 2). *Fraxinus platypoda* was treated by Wallander (2008) within sect. *Fraxinus* while she placed *F. chiisanensis* and *F. spaethiana* as *incertae sedis*; these three Asian species differ from North American sect. *Melioides* in their polygamous sexual condition (vs. strict dioecy in the North American species) and flavonoid chemistry (Lee et al. 2012). Wallander reviewed other evidence (mainly floral morphology and leaf flavonoids) relative to the phylogenetic position of these species. In a formal classification, these three could reasonably be treated either as a separate section or as a part of sect. *Melioides*.

(b) The American *F. cuspidata* was regarded by Jeandroz et al. as a member sect. *Dipetalae*, by Wallander as "incertae sedis." A consensus tree in the Jeandroz et al. analysis (their Figure 4, excerpted here as Figure 3) positioned *F. cuspidata* as sister to North American sect. *Melioides*. The Wallander analysis (sect. *Melioides* excerpted here as Figure 4) positioned *F. cuspidata* as sister to *F. spaethiana*, within the same clade of three Asian species as identified by Hinsinger et al. In the Hinsinger et al. analysis (their Figure 2, and as represented here in Figure 1), however, *F. cuspidata* is sister to the North American/Asian pair of clades. Following Wallander's suggestion, a case could be

made for treating *F. cuspidata* as a monotypic section, based on its apparently isolated phylogenetic position and distinctive morphology (flowers bisexual and anemophilous, petals 4, white, united in a tube 2–3 mm, lobes linear, 5–6 mm).

Within sect. *Melioides*, five informal groups are recognized here (Table 1). Among the eastern and southwestern North American species, the Americana Group (the white ash group) is highly distinctive in morphology, with the abaxial leaf surfaces completely covered by a waxy reticulum — this structure is viewed here as a single-origin feature indicating that at least the genome underlying this epidermal expression in the Americana Group is monophyletic. In all of the other species, the epidermis of the abaxial leaf surface is exposed, without wax, as also in all other species of the genus. *Fraxinus uhdei* (Mexico and Central America) and *F. latifolia* (Pacific coast region) are set apart here as the Uhdei Group and the Latifolia Group because of their geographic disjunctions and because there seems to be agreement among the molecular analyses (Figs. 2, 3, 4) that neither species arose from within the Pennsylvanica Group as recognized here, which essentially comprises the remainder of the species.

Among the three published phylogenetic hypotheses for sect. *Melioides*, the most unexpected species placements reflect an apparent lack of coherence among the species of the Americana Group — their dispersal among species of other groups suggests that either misidentifications or speciation by hybridization, or both, are reflected in the cladogram topologies. An alternative hypothesis, subjectively developed mostly on the basis of morphology and geography, and with attention to consistencies in the molecular analyses, is presented here (Fig. 1) to summarize what seems plausible and perhaps to serve as a guide or model in further investigations.

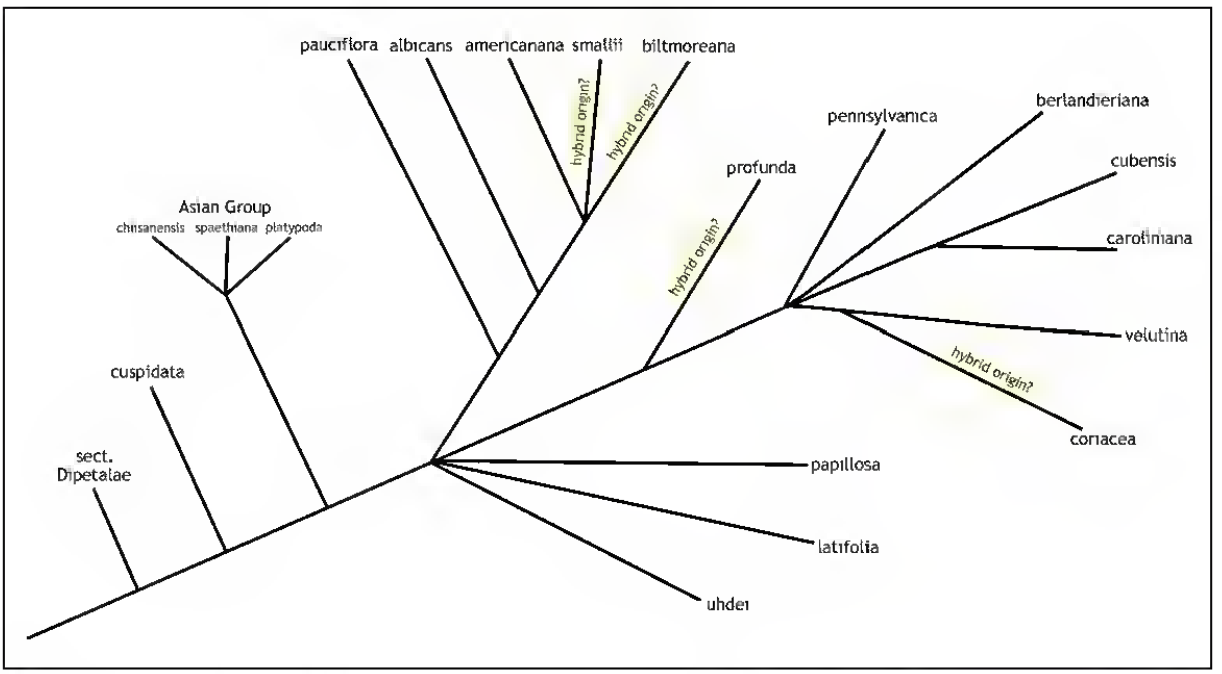

Figure 1. Hypothetical, subjectively formulated phylogeny, based on morphology and geography, of sect. *Melioides*. *Fraxinus cuspidata* and the Asian group are generally indicated by the molecular phylogenies to have a sister or basal relationship to the traditionally recognized North American species of the section. The position of sect. *Dipetalae* as basal in the whole genus is indicated by both Wallander and Hinsinger et al. *Fraxinus smallii* (tetraploid), *F. biltmoreana* (hexaploid), and *F. profunda* (hexaploid), and perhaps *F. coriacea* (tetraploid) may be of hybrid origin.

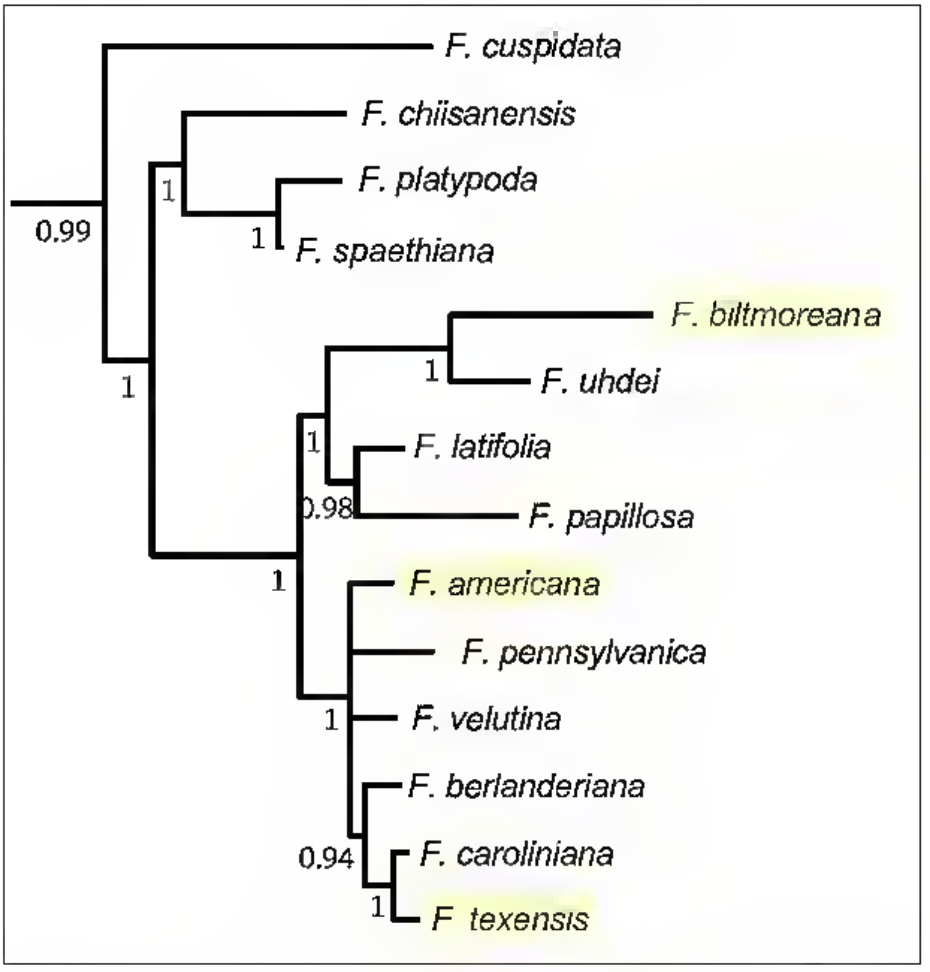

Figure 2 Phylogeny of sect *Melioides* extracted from Figure 1 of Hinsinger et al (2013), which shows a Bayesian analysis of the combined dataset (cpDNA, ETS, ITS and phantastica) Posterior probabilities ≥0 50 are indicated below the branches The yellow highlighted samples of *F. americana* and *F. texensis* appear to be out of place within the clade that otherwise comprises red ash species — based on morphology they would be expected to cluster with *F. biltmoreana* (also yellow highlighted) In any case, apart from *F. latifolia* and *F. uhdei*, the subjective and arbitrary sample selection involved in the derivation of this tree appears to render it essentially meaningless (see text)

Identifications

In recent studies of *Fraxinus*, I found that a significant proportion of herbarium specimens of North American *Fraxinus* have been misidentified, even in collections amassed or curated by experienced taxonomists This is especially true for sect *Melioides*, where *F. americana* and *F. pennsylvanica* commonly are confused While this might suggest that taxonomic distinctions can be subtle, it does not indicate that the species are indistinct Implicit here is the notion that species boundaries can be discerned among the ash species, and having intensively studied the North American taxa (Nesom 2010a–h, Nesom submitted, Williams & Nesom 2010), I believe this is possible, even though some of the species are variable A possible exception to this has been in the attempt to understand the pattern of variation in the *F. velutina papillosa* complex — *F. papillosa* is re-segregated here, based in part on reconsideration of molecular evidence (see comments below)

The 57 North American sect. *Melioides* samples of Hinsinger et al. were mostly from arboreta (mostly European, some in the USA), in two species (*F. berlandieriana*, *F. papillosa*); sampling was augmented by herbarium specimens (total of 5) from MEXU. Of the 52 total arboretum collections, 33 were vouchered (specimens deposited at P). By sampling multiple individuals for each taxon, they "expected that, if hybridization or misidentification occurred, only one or a few individuals in a particular species would be affected, as a consequence, most individuals would still be classified in a monophyletic group representative of the species." Such did not prove to be the case for North American sect. *Melioides*, however, as inconsistency of phyletic position for samples within a single taxon was a significant feature of the analyses of individual data sets where all samples are shown (the maximum likelihood analyses). It seems a reasonable guess that arboretum identifications were accepted at face value in the Hinsinger et al. study, since who among the authors might have provided confirmations of identity was not indicated.

The maximum likelihood (ML) analyses of Hinsinger et al. include all of their samples (see Figs. S2, S3, S4 in their Supporting Information). Their Bayesian (BIM) analyses, however, including that of the combined dataset shown in their Figure 1 (Fig. 2 above), were done with a reduced dataset. "All BIM analyses were performed on a reduced dataset using MrBayes. This reduced dataset was created by using one individual per species following Wallander, with the selection of individuals located within **the ML tree** [emphasis added] at positions that were reasonable considering their identity for each data partition, that is, grouping with other individuals from the same species" (pp. 4–5). Presumably they meant "the ML trees" (S2, S3, S4). But whether they used a single (unspecified) ML tree or all three, their process of dataset reduction for sect. *Melioides* appears to have been almost entirely subjective. Positions on the S4 tree seem utterly random for all samples. On the S2 and S3 trees, the only species that cluster unambiguously are *F. latifolia* and *F. uhdei* — for species where half or more than half of the samples are clustered and the single sample was selected from the largest cluster. *F. velutina* is the only candidate. All other choices appear arbitrary.

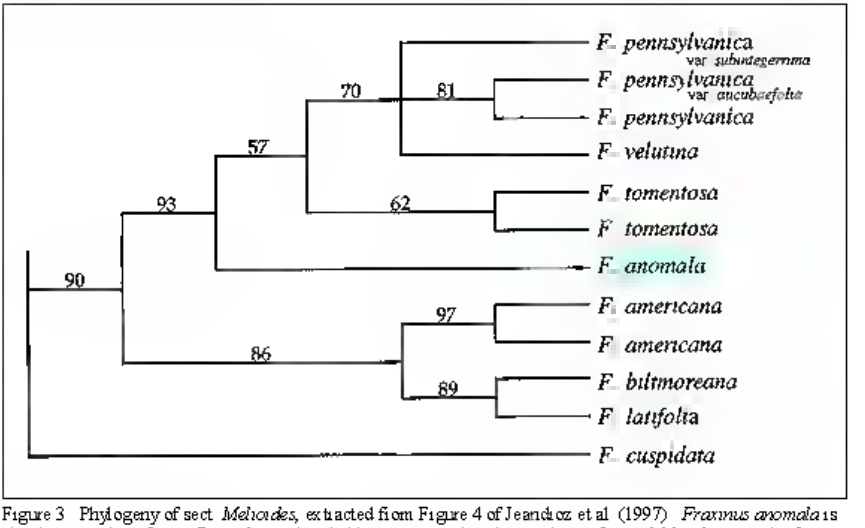

Figure 3. Phylogeny of sect. *Melioides*, extracted from Figure 4 of Jeandroz et al. (1997). *Fraxinus anomala* is clearly a member of sect. *Dipetalae* and probably appears within the topology of sect. *Melioides* a result of misidentification.

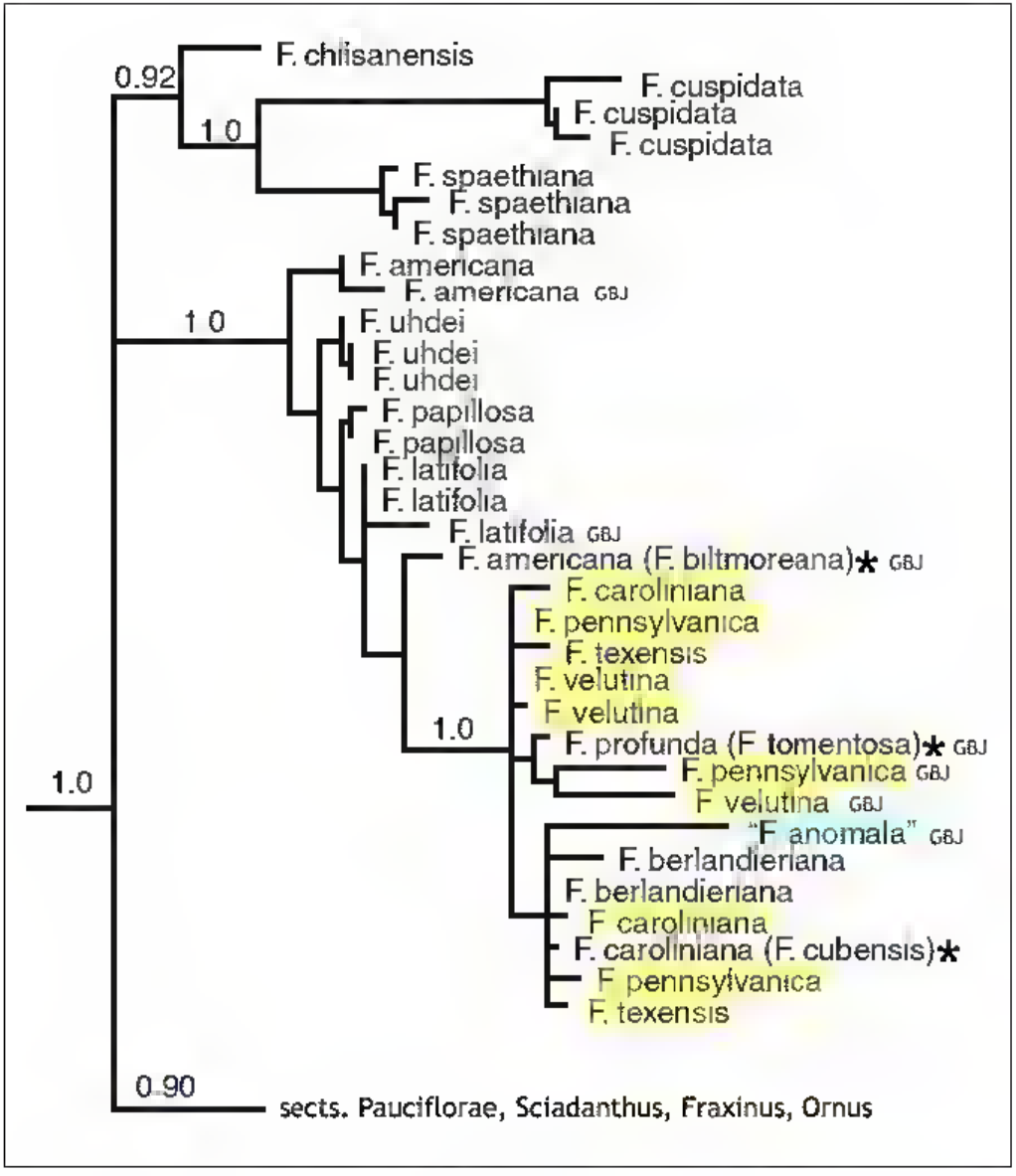

Figure 4 Phylogeny of sect *Melioides* extracted from Figure 1 of Wallander (2008) which portrays a majority rule consensus tree resulting from the Bayesian analysis of 111 ITS sequences representing 40 Fraxinus species and five Oleaceae outgroup species Bayesian posterior probabilities are shown above the branches Starred samples are species represented by only one sample Yellow highlighted samples represent species placed in positions separated from one another, probably indicating either hybridization or misidentification "GBJ" indicates a GenBank sequence originally used in the Jeandroz et al analysis The "F anomala" sample almost certainly is misidentified as recognized by Wallander

All of the sect. *Melioides* samples in the Jeandroz et al. analysis are noted as having originated from the Montreal Botanic Garden. Vouchers apparently were not made for those samples or any others in the study.

Wallander's samples of sect. *Melioides* were from cultivated trees at arboreta (Missouri Botanical Garden, Kew Garden, vouchers at GB), field collections from Oregon and Washington (*F. latifolia*, vouchers at GB), herbarium specimens (GB, MO, NY, S), and GenBank data (1 sample of *F. pennsylvanica*, 1 of *F. profunda*, 1 of *F. velutina*).

The Americana group

The Americana Group is distinctive in the waxy reticulum overlying the abaxial leaf surface, a feature without parallel elsewhere in the genus (or, apparently, elsewhere in the family).

* *Fraxinus albicans* (= *F. texensis*; chromosome number unreported) is closely similar to diploid *F. americana* — the main differences are in leaf and fruit size and geography (Nesom 2010b). If *F. albicans* proves to be diploid, without hybrid origin, then it is unexpected that *F. albicans* should be placed apart from *F. americana* in the Wallander analysis (Fig. 4) and, further, that its two samples should be in separated positions. In any case, a duplicate of the voucher for "texensis2" (TEX; from Coryell Co., Texas; in the "upper" position in Fig. 4) indeed is correctly identified.

* *Fraxinus smallii* (tetraploid) and *F. biltmoreana* (hexaploid) presumably include the genome of diploid *F. americana* and it is reasonable to speculate that their extra chromosome sets were acquired via hybridization with forms of *F. pennsylvanica* or some other species of green ash. Such interspecific hybridization might account for the seemingly disparate phylogenetic positions of these species in molecular analyses. Or the ancestry of *F. smallii* and *F. biltmoreana* may have involved species of the Americana Group no longer extant. *Fraxinus smallii* differs from *F. americana* mostly in fruit size and petiole shape and the former may have originated as an autopolyploid or segmental allopolyploid. No data exists at present to support any hypothesis of reticulate evolution in sect. *Melioides*.

* *Fraxinus pauciflora* (Nesom 2010c) is distinct in geography, ecology, and morphology and is placed here (Fig. 4) as sister to the other white ash species — its chromosome number is unreported.

The Pennsylvanica Group

The Pennsylvanica Group is shown as monophyletic in Figure 4, but a clear morphological synapomorphy is not evident. The group is spread over eastern North America and central and southwestern states of the USA.

* *Fraxinus profunda* is distinct in its extremely large fruits and leaves, deep swamp ecology, and hexaploid constitution (Nesom 2010h) — it may be of hybrid origin, similar to the possibilities for *F. smallii* and *F. biltmoreana*.

* *Fraxinus pennsylvanica* is variable over its wide range and numerous segregates have been named, but a clear concept of morpho-geographic subentities has never been documented.

* *Fraxinus velutina* (Nesom 2010f; Williams & Nesom 2010) also is variable over a wide range. It apparently intergrades with *F. papillosa*, but this needs to be studied in detail.

* *Fraxinus coriacea* sometimes has been considered conspecific with *F. velutina* but is geographically and morphologically distinct (Nesom 2010e). Taylor (1945) reported a tetraploid chromosome count for *F. coriacea* (as "F. velutina var. coriacea"), in contrast to four diploid collections of *F. velutina* (reported as "F. velutina," "F. velutina var. glabra," and "F. velutina var. toumeyi").

* *Fraxinus caroliniana* and *F. cubensis* apparently are a sister pair with contiguous geographic ranges (Nesom 2010c). One of the two samples of *F. caroliniana* ("caroliniana1," from Florida) in Wallander's analysis is positioned close to *F. cubensis* but the other ("caroliniana2," from North Carolina) is separated (see Fig. 4). The "caroliniana2" sample (voucher at MO) is confirmed here as correctly identified as *F. caroliniana*.

* *Fraxinus berlandieriana* has sometimes been synonymized with *F. pennsylvanica* and perhaps is most closely related to it (Nesom 2010f). The tendency of *F. berlandieriana* to produce 3-winged fruits also is characteristic of *F. caroliniana*/*cubensis* but morphological dissimilarities suggest that this probably is a parallelism. One of Wallander's samples of *F. berlandieriana* was from Texas (*Jones 3595*, NY), the other from Hidalgo, Mexico (*Pringle 13584*, S) — the type of *F. pringlei* (*Pringle 9417*, valley near Dublan, Hidalgo) is from a tree similar to *Pringle 13584*. *Fraxinus pringlei* probably is justifiably treated as conspecific with *F. berlandieriana* (contrary to a prior assertion of mine; Nesom 2010f), but this needs study.

Monotypic species groups

Fraxinus papillosa. This has sometimes been compared with *F. americana* (see review comments in Williams and Nesom 2010) but it was tentatively considered a regional expression of *F. velutina* (Williams & Nesom; Nesom 2010). The whitened abaxial leaf surface of *F. papillosa* does not have the reticulate overlay of wax like that of the Americana group — each abaxial epidermal cell of *F. papillosa* is abruptly convex and formed upward into a short-cylindric, papilla-like structure (see SEMs in Williams and Nesom) with no obvious evidence of deposition of white-colored material. The white color perhaps due to increased reflectivity of the raised cells. Typical *F. velutina*, which has abaxial epidermal cells with green, relatively flat surfaces, appears to intergrade with *F. papillosa*, but the difference in morphological extremes is so great that the two probably would better be regarded as separate but intergrading species.

The molecular studies of Wallander (2008) and Hinsinger et al. (2013), based on independent sampling, suggest that *Fraxinus papillosa* is more closely related to *F. latifolia*, *F. uhdei*, and *F. americana* than to the Pennsylvanica Group. Although the abaxial epidermis of *F. papillosa* and *F. americana* are radically different in morphology, it seems reasonable to speculate that they may be homologous, in the sense that the same alleles underlie the shifts away from the "ground-plan" epidermis characteristic of the rest of the genus.

Fraxinus uhdei and *Fraxinus latifolia*. Results of the three molecular studies consistently indicate that these two species are not members of the Pennsylvanica Group in the concept here. Relationships of these two species with the Americana Group and *F. papillosa* are not unambiguously resolved.

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CORYDALIS INCISA (FUMARIACEAE) IN BRONX AND WESTCHESTER COUNTIES, NEW YORK

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ABSTRACT

Spontaneously growing plants of the East Asian *Corydalis incisa* (Thunb.) Pers. (Fumariaceae) are reported from Westchester Co., New York, for the first time. The species was previously only known from a small area along the Bronx River in Bronx Co., New York. The Westchester County plants documented here represent the second known wild population in North America. This discovery increases the number of *Corydalis* species in North America from ten to eleven and from four to five in the northeastern USA. It is the only spontaneous, purple- or white-flowered species in the Northeast.

Corydalis incisa (Thunb.) Pers growing outside of cultivation in North America were first discovered on the floodplain of the Bronx River, near the Burke Avenue Bridge in Bronx Park, New York, by Michael Sundue during the 2005 Bronx River BioBlitz (Sundue, pers. comm). No voucher specimens were collected. Soon after, Steve Glenn collected the species at the same locality and noted "dozens" of individuals along both banks of the River, reported for the first time as naturalized in North America by Lamont et al. (2011). The population has since persisted and expanded. In 2014, a second population was discovered by the authors and is detailed below.

In 2010, Daniel Atha found one plant, sterile at first (*Atha 6925*) and then in flower (*Atha 7021*) on the grounds of The New York Botanical Garden and later the same year, he and Rob Naczi visited the original 2005 BioBlitz site, about 1000 meters north and found the plants thriving along both banks of the river.

The genus *Corydalis* (Fumariaceae) comprises 450–465 species (Tebbitt et al. 2008; Zhang et al. 2008), most of which are native and endemic to China (Tebbitt et al. 2008; Lidén & Zetterlund 1997). There are currently thirty-five recognized sections (Tebbitt et al. 2008). *Corydalis* sect. *Incisae* Fedde is characterized by the presence of tubers and pendent capsules from patent pedicels (Zhang et al. 2008). The section consists of nine species, eight of which are endemic to China (Zhang et al. 2008). *Corydalis incisa* is the one species of the section native outside of China. It is said to be "widespread and common" in Korea, Taiwan, and eastern China (Tebbitt et al. 2008). Within sect. *Incisae*, *C. incisa* is distinguished by its deeply incised leaflet lobes, racemes with 5–15 flowers, sepals 1–2 mm long, spur straight, and fruits narrowly oblong to linear (Zhang et al. 2008).

Ten species of the genus are reported for the Flora of North America North of Mexico (Stern 2007). In the flora area of the Manual of Vascular Plants of Northeastern United States and adjacent Canada, four species are reported (Gleason & Cronquist 1991). In the Northeast, three species have yellow flowers and one has pink flowers (*Corydalis sempervirens* (L.) Pers.). *Corydalis incisa* is the only species with purple flowers native or naturalized in the northeastern USA.

Corydalis incisa (Thunb.) Pers.

Biennial herb, glabrous, 10–50 cm tall; the sap watery; leaves ternate to bi- or tri-ternate; ultimate segments rhombic, the bases cuneate, the margins deeply incised, first-year plants from fusiform tuber ca 12 × 5 mm, leaves few, reduced, second-year plants from fibrous roots, erect to ascending, branched, leaves usually numerous, the petioles 5–20 cm long, the blades 4–12 × 4–12 cm; upper-most leaves reduced near the inflorescence; racemes erect, 6–9 cm long (in fruit), bracteate, the bracts rhombic, incised 4–10 mm long; flowers 10–16 per raceme; pedicels 10–15 m long, patent; sepals reduced, lacerate; corolla tubular, 8–15 mm long, the petals connivent, purple (rarely white), dilated and darker at the apex, saccate at the base, capsules pendent, oblong, 12–18 × 3 mm, green, explosively dehiscent, seeds ca 1 mm long. Flowering and fruiting May to June. (The description is derived from field observation in New York and study of preserved Asian specimens at NY).

Vouchers. **New York**. Westchester Co.: Crestwood, Bronx River Reservation, between the Bronx River Parkway and Dale Road at about Cross Hill Road, in the annual floodplain forest of the Bronx River with *Acer saccharinum*, *Acer saccharum*, *Acer negundo* and *Morus alba* in the overstory and *Reynoutria japonica*, *Rosa multiflora* and *Laportea canadensis* dominating the understory, 40.965898 N, 73.818284 W (±25 m), 31 m, 10 Jun 2014, *Atha 14519* (NY). Data will be available online through the C.V. Starr Virtual Herbarium (2014). All other vouchers cited are at NY.

Inspired by Linda Rohleder of the New York-New Jersey Trail Conference and Steve Young of the New York Natural Heritage Program, the authors conducted a rapid survey of the original sites to assess the current extent of the population. The survey, conducted in May and June of 2014, revealed scattered individuals of mostly second-year plants around the Magnolia Way Bridge at the north end of The New York Botanical Garden (*Atha 14402, 14403, 14406, 14407*). No plants were found further south in the Garden, perhaps because the banks are rocky and unsuitable for germination.

At the original site in Bronx Park, as reported by Lamont et al. (2011), north of the Garden, the survey confirmed dense stands on both sides of the river, extending throughout the annual floodplain. The population consisted of both first-year seedlings and second-year flowering and fruiting plants (*Atha & Lumban Tobing 14408, 14410, 14411, 14412, 14413, 14414*). Within one heavily infested area, 32 seedlings were counted in an area of 10 cm^2 (*Atha & Lumban Tobing 14414*) and Figure 1.

The authors also discovered a previously undocumented population 11.5 kilometers northeast in the Bronx River Reservation of Westchester County, representing the second known population in North America and the first report of the species for Westchester County (USDA, NRCS 2014; Weldy & Werier 2014). The sighting was immediately reported to Westchester County Parks Department and the population was vouchered (*Atha 14519*).

Corydalis incisa appears to thrive on fine, alluvial sediments, competing with native riparian understory plants including *Persicaria virginiana*, *Ageratina altissima*, *Impatiens capensis*, *Laportea canadensis*, and woody seedlings. The very aggressive *Ficaria verna* and *Reynoutria japonica* were also present and abundant (Fig. 2). When very young, *C. incisa* plants resemble *Anthriscus sylvestris*, *Artemisia vulgaris*, *Cryptotaenia canadensis*, and *Osmorhiza claytonia*, all of which may grow abundantly in the same habitat.

It is not known how the species became established in the wild, but given the plant's limited range and its biological traits, we suspect that they were first cultivated in Westchester County near the Bronx River. The fruits are explosively dehiscent and we suspect that seeds were dispersed downriver during floods. The plants quickly flower, fruit, disperse their seeds and then die back, leaving no trace above ground. The first-year tubers may also be dispersal agents.

Figure 1. *Corydalis incisa*. Seedlings (*Atha & Lumban Tobing 14414*, NY). Note scale in centimeters

Figure 2. *Corydalis incisa*. Mature second-year plant (*Atha & Lumban Tobing 14408*, NY)

Figure 3 *Corydalis incisa*. Mixed population of purple- (*Atha & Lumban Tobing 14413*, NY) and the rare white -flowered (*Atha & Lumban Tobing 14412*, NY) forms

In one of the densest stands along the west bank of the Bronx River we found three plants with entirely white flowers (*Atha & Lumban Tobing 14412*). The plants were otherwise morphologically identical to sympatric plants with purple flowers (*Atha & Lumban Tobing 14413* and Figure 3). The white flowered form has been named *Corydalis incisa* var. *alba* S.Y. Wang.

The New York Botanical Garden, the New York City Department of Parks and Recreation (NYC Parks), the Bronx River Alliance, and the Westchester County Parks Department are working in collaboration with the Lower Hudson Partnership for Regional Invasive Species Management (Lower Hudson PRISM) to assess the extent of the invasion and determine how it should be monitored and managed in the future. Thain Family Forest staff of The New York Botanical Garden weeded the plants in the Garden this year and will continue to monitor and manage the species in the future. NYC Parks staff members have made plans to hand-pull second-year plants before they fruit and disperse their seeds next year.

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PLUCHEA FOETIDA (ASTERACEAE) CONFIRMED IN THE OKLAHOMA FLORA

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ABSTRACT

Pluchea foetida is confirmed as a member of the native flora of Oklahoma. It is documented by three collections from the West Gulf Coastal Plain of Pushmataha County, apparently at the northwestern edge of the distribution of the species. Collections were made during the summer of 2008 and 2014.

Pluchea foetida (L.) DC. var. *foetida* (Asteraceae, Plucheeae), commonly called stinking camphorweed, is distributed in permanently wet soil of the southeast coastal plain of the USA (New Jersey to south Florida, west to south Arkansas, and east Texas (Cronquist 1980). Nesom (2006) included Hispaniola and Mexico (as have Small 1933 and Fernald 1950) and southeast Oklahoma as part of the distribution in his treatment of *Pluchea* for the Flora of North America. The purpose of this paper is to elucidate the distribution of the species in Oklahoma.

Despite being mentioned by Nesom (2006) as occurring in Oklahoma, *Pluchea foetida* is not included in the Keys to the Flora of Oklahoma (Waterfall 1966), the checklist of the flora of the state (Taylor and Taylor 1994), or Keys and Descriptions for the Vascular Plants of Oklahoma (Tyrl et al. 2010), nor is it mapped as part of the Oklahoma flora in USDA, NRCS (2014) or Kartesz (2014). Inquiries to the herbaria most likely expected to possess a specimen (BRIT-SMU, CSU, DUR, UCO, OKL, OSU, TAMU, TEX-LL, and TULS) were successful in locating one specimen at OKL (Hoagland et al. 2004).

Based upon specimens cited below, which were recently collected, *Pluchea foetida* is now documented as part of the flora of Oklahoma.

Voucher specimens. **USA. Oklahoma.** Pushmataha County: Junction of Indian Nation Turnpike and Hwy 3, ca. 0.3 mi N of junction of Indian Nation Turnpike/Hwy 3, E side, 28 Aug 2008, *Buthod* and *Hoagland* 7843 (OKL); 0.4 mi N of the jct of OK Hwy 3 and Indian Nation Turnpike on Indian Nation Turnpike in hillside bog in right of way on the E side of Indian Nation Turnpike (34° 14'25.78" N, 95° 39'8.95" W), 8 Jul 2014, *J., L., A., and R. Singhurst 20,825* (BAYLU, OKL); Jct. of OK Hwy 3 and Indian Nation Turnpike, in hillside bog in right of way on NE corner inside cloverleaf adjacent to turnpike pay facility (34° 14'14.72" N, 95° 39'1.26" W), 9 Aug 2014, *J., L., A., and R. Singhurst 20,826* (BAYLU, OKL). Figures 1 and 2.

Figure 1. Photo of capitula of *Pluchea foetida* in Pushmataha Co., Oklahoma. Photo by Jason Singhurst.

Figure 2. Habitat photo of *Pluchea foetida* in hillside bog in Pushmataha Co., Oklahoma. Photo by Jason Singhurst.

The nearest documented occurrences to the reported Oklahoma *Pluchea foetida* records include the following: (1) Miller Co., Arkansas, *Reid 1511*, UARK, which is approximately 215 km at 123° from the Oklahoma locations, and (2) Smithland in Marion Co., Texas, *Singhurst & Adams 18934*, BAYLU, which is about 250 km at 145° from the Oklahoma stations. The cited Oklahoma occurrences apparently represent the northwestern limits of the distribution of the species.

In Pushmataha County, *Pluchea foetida* appears restricted to Oklahoma Acidic Hillside Seeps (Nature Serve 2014) surrounded by the Antlers Sand Formation. These hillside seeps are highly localized and isolated wetlands in southeast Oklahoma that include a number of disjunct West Gulf Coastal Plain flora at their northwest range limits. Dominant species of Oklahoma Acidic Hillside Seeps include *Andropogon virginicus*, *Dichanthelium scoparium*, *Boehmeria cylindrica*, *Sphagnum* spp., and *Polytrichum commune*. Other characteristic flora of the two hillside seeps include *Baccharis halimifolia*, *Drosera brevifolia*, *Carex* spp., *Cyperus strigosus*, *Eleocharis tortilis*, *Eriocaulon decangulare*, *Eupatorium perfoliatum*, *E. rotundifolia*, *Gratiola pilosa*, *Hydrolea ovata*, *Juncus validus*, *Helianthus angustifolius*, *Lycopodiella appressa*, *Ludwigia hirtella*, *Mitreola petiolata*, *Osmunda cinnamomea*, *O. regalis*, *Oxypolis rigidior*, *Rhexia mariana*, *R. virginica*, *Rhynchospora caduca*, *R. gracilenta*, *R. rariflora*, *Rubus argutus*, *Scleria sp.*, *Utricularia juncea*, *U. rariflora*, *U. subulata*, *Xyris difformis*, and *X. jupicai*.

Pluchea foetida will be ranked S1 by the Oklahoma Natural Heritage Inventory, indicating that it is "critically imperiled in the state because of extreme rarity or because of some factor(s) such as very steep declines in populations making it especially vulnerable to extirpation from the jurisdiction" (Oklahoma Natural Heritage Inventory 2014; NatureServe Explorer 2014).

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ATLAS OF THE FLORA OF NEW ENGLAND: FAMILIES OF VOLS. 9-13 AND 15-16 (EXCEPT FABACEAE & ROSACEAE) OF THE FLORA OF NORTH AMERICA SERIES

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ABSTRACT

Dot maps are provided to depict the county level distribution of the Magnoliophyta taxa growing outside of cultivation in the six New England states of the northeastern USA for families in volumes 9-13 and 15-16 (except Fabaceae and Rosaceae) of the Flora of North America series. Families included are Anacardiaceae, Apiaceae, Araliaceae, Balsaminaceae, Boraginaceae, Celastraceae, Cornaceae, Elaeagnaceae, Euphorbiaceae, Geraniaceae, Haloragaceae, Hydrangeaceae, Hydrophyllaceae, Lamiaceae, Linaceae, Lythraceae, Oleaceae, Onagraceae, Oxalidaceae, Polemoniaceae, Polygalaceae, Rhamnaceae, Rutaceae, Sapindaceae, Verbenaceae, Vitaceae, and other small families. The maps treat 527 taxa (species, subspecies, varieties, and hybrids, but not forms) based primarily on specimens in the major herbaria of Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut, with most data derived from the holdings of the New England Botanical Club Herbarium (NEBC). Brief synonymy (to account for names used in standard manuals and floras for the area and on herbarium specimens), habitat, chromosome information, and common names are also provided.

This article is the fourteenth and last in a series (Angelo & Boufford 1996, 1998, 2000, 2007, 2010, 2011a, 2011b, 2012a, 2012b, 2012c, 2013a, 2013b, 2014) that presents the distributions of the vascular flora of New England in the form of dot distribution maps at the county level (Figure 1). The atlas is posted on the internet at <http://neatlas.org>, where it will be updated as new information becomes available.

This project encompasses all vascular plants (lycophytes, pteridophytes and spermatophytes) at the rank of species, subspecies, and variety growing in reproducing populations outside of cultivated habitats in the six New England states. Hybrids are also included, but forms and other ranks below the level of variety are not. The dots are based on voucher specimens primarily in New England herbaria (of colleges, universities, botanical gardens, and public museums). This fourteenth installment includes the families that will be included in volumes 9-13 and 15-16 (except Fabaceae and Rosaceae) of the Flora of North America North of Mexico (FNANM) series. Of the 527 taxa treated, 306 are not native to the region.

The habitat data are distillations from a variety of sources augmented by our own field observations. An attempt was made to indicate habitat information as it applies to a particular taxon in New England rather than to the entire range of the taxon. Habitat information is not provided for hybrid taxa.

It is our hope that these articles will stimulate additional field work to supplement the distributions portrayed in the maps. The New England Botanical Club herbarium has proven to be the most important resource for this project. We are eager to receive information on voucher specimens in

public herbaria documenting range extensions and filling county gaps in distributions. Similarly, because the atlas of the New England flora will be continuously updated as new information becomes available, we are eager to receive notification of published corrections of cytological information and new, documented chromosome counts for taxa in the New England flora.

MATERIALS AND METHODS

Materials and methods are as outlined in Angelo and Boufford (1996) and in a web version (Angelo & Boufford 2011c) and are not repeated here.

TAXONOMY AND FORMAT

The taxonomy and nomenclature adopted for this work primarily follow that of draft treatments for the Flora of North America project and checklists of accepted taxa of The Flora of North America Expertise Network, except that families, genera, and species are arranged alphabetically. The families and their circumscription do not necessarily reflect current views on relationships or composition. The Angiosperm Phylogeny Website (Stevens 2001 onwards) should be consulted for a continuously updated treatment of families and their inclusive genera. Named and unnamed hybrid taxa are placed alphabetically at the end of the genus in which they occur. Unnamed hybrids combine the names of the progenitors alphabetically by epithet. Taxa that are not native to New England are indicated by uppercase text. Unpublished names are not used, even if publication is pending.

Chromosome numbers are taken primarily from draft treatments for the Flora of North America project, Gleason and Cronquist (1991), and from Goldblatt and Johnson (1979–).

Synonymy is provided primarily with respect to names accepted in standard manuals covering New England published from 1950 onward, including Fernald (1950), Gleason and Cronquist (1991), and Seymour (1982) and on herbarium labels in New England herbaria. Synonyms have not been provided where the distribution for the synonymized name does not include New England.

The following list (which includes excluded taxa) will aid readers in finding familiar names that have been transferred to other taxa:

Acanthopanax	=>	*Eleutherococcus*
ACERACEAE	=>	*SAPINDACEAE*
Anchusa (in part)	=>	*Cynoglottis*
APIACEAE (in part)	=>	*ARALIACEAE*
Calylophus	=>	*Oenothera*
Coelopleurum	=>	*Angelica*
CORNACEAE (in part)	=>	*NYSSACEAE*
Crotonopsis	=>	*Croton*
Epilobium (in part)	=>	*Chamaenerion*
Gaura	=>	*Oenothera*
Gilia (in part)	=>	*Ipomopsis*
HIPPOCASTANACEAE	=>	*SAPINDACEAE*
HYDROCARYACEAE	=>	*LYTHRACEAE*
Isanthus	=>	*Trichostema*
LABIATAE	=>	*LAMIACEAE*
Lithospermum (in part)	=>	*Buglossoides*
LORANTHACEAE	=>	*VISCACEAE*
Lycopsis	=>	*Anchusa*

Onosmodium	=>	*Lithospermum*
Rhamnus (in part)	=>	*Frangula*
Rhus (in part)	=>	*Toxicodendron*
SANTALACEAE (in part)	=>	*COMANDRACEAE*
Satureja (in part)	=>	*Clinopodium*
SAXIFRAGACEAE (in part)	=>	*CELASTRACEAE*
SAXIFRAGACEAE (in part)	=>	*HYDRANGEACEAE*
TRAPACEAE	=>	*LYTHRACEAE*
UMBELLIFERAE (in part)	=>	*APIACEAE*
UMBELLIFERAE (in part)	=>	*ARALIACEAE*
Verbena (in part)	=>	*Glandularia*

The following species have been reported from our area but are excluded for the reasons noted:

ACER PALMATUM Thunberg [no voucher of a population in the wild found; reported from various counties in Connecticut, Massachusetts and Rhode Island]

AGASTACHE RUGOSA (Fischer & C.A. Meyer) Kuntze [no voucher of wild occurrence found; reported from Massachusetts]

AMPELOPSIS ACONITIFOLIA Bunge [no voucher found; reported from New London County, Connecticut, and Massachusetts]

AMPELOPSIS HUMILIFOLIA Bunge [no voucher of wild occurrence found; reported on the grounds of the Arnold Arboretum in Suffolk County, Massachusetts]

AMSINCKIA SPECTABILIS Fischer & C.A. Meyer [voucher for this is misidentified specimen of *AMSINCKIA MENZIESII* (Lehmann) A. Nelson & J.F. Macbride; reported from Middlesex County, Massachusetts]

ASTRANTIA MAJOR Linnaeus [no voucher of wild occurrence found; reported from Worcester County, Massachusetts]

BALLOTA NIGRA Linnaeus var. *ALBA* (Linnaeus) Tinant [no voucher found; reported from New Haven County, Connecticut]

BUPLEURUM ODONTITES Linnaeus [no voucher of wild occurrence found; reported from Essex County, Massachusetts]

BUXUS SEMPERVIRENS Linnaeus [no voucher of wild occurrence found; reported from Newport County, Rhode Island]

CARDIOSPERMUM HALICABABUM Linnaeus var. *HALICABABUM* [no voucher of wild occurrence found; reported from Connecticut, and Middlesex County, Massachusetts]

CHAEROPHYLLUM TAINTURIERI Hooker [no voucher found; reported from Rhode Island]

CLINOPODIUM NEPETA (Linnaeus) Kuntze subsp. *GLANDULOSUM* (Requien) Govaerts (*C. CALAMINTHA* (Linnaeus) Kuntze; *SATUREJA CALAMINTHA* (Linnaeus)

Scheele var. *GLANDULOSA* (Requien) Briquet) [no voucher found; reported from Kent County, Rhode Island]

Collinsonia punctata Elliott (*C. canadensis* var. *punctata* (Elliott) A. Gray) [no voucher found; report apparently based on misidentified voucher; reported from New London County, Connecticut]

CORNUS KOUSA Bürger *ex* Miquel [no voucher of wild occurrence found; reported from Fairfield County, Connecticut]

CROTON HEPTALON (Kuntze) B.W. van Ee & P.E. Berry [no voucher found; reported from Suffolk County, Massachusetts]

CUMINUM CYMINUM Linnaeus [no voucher of wild occurrence found; reported from Suffolk County, Massachusetts]

CYMOPTERIS GLOMERATUS (Nuttall) de Candolle [reported in error from Rockingham County, New Hampshire; report based on an article on this western species in Rhodora 107:359 (2005) confusing it with the report of a new record of *Hibiscus moscheutos* from Rockingham County, New Hampshire in the same issue.]

CYNOGLOSSUM WALLICHII G. Don [no voucher of wild occurrence found; reported as adventive in a garden in Worcester County, Massachusetts]

DRACOCEPHALUM THYMIFLORUM Linnaeus [no voucher found; reported in wool waste from Middlesex County, Massachusetts]

ELAEAGNUS PUNGENS Thunberg [no voucher of established wild population found; reported as waif in Plymouth County, Massachusetts]

EPILOBIUM PARVIFLORUM Schreber [no voucher found; reported Washington County, Vermont]

ERODIUM LACINIATUM (Cavanilles) Willdenow var. *BOVEI* (Delile) Murbeck [no voucher found; reported in 1918 in wool waste in Middlesex County, Massachusetts]

EUONYMUS OBOVATUS Nuttall [no voucher of wild occurrence found; reported from Suffolk County, Massachusetts based on citation of occurrence on grounds of Arnold Arboretum]

EUONYMUS PHELLOMANUS Loesener [no voucher of wild occurrence found; reported from Fairfield and New Haven Counties, Connecticut, and from Norfolk County, Massachusetts]

Euphorbia ipecacuanhae Linnaeus [no voucher found; historic collections of this are reported in the literature from Hartford County, Connecticut]

EUPHORBIA PUBENTISSIMA Michaux (*E. COROLLATA* Linnaeus var. *MOLLIS* Millspaugh) [voucher is misidentified *E. COROLLATA* (typical); reported from Coös County, New Hampshire]

EUPHORBIA SERPENS Kunth [only cited voucher collected in garden; reported from Belknap County, New Hampshire]

EUPHORBIA SERPYLLIFOLIA Persoon var. *SERPYLLIFOLIA* [no voucher found; reported from New Hampshire]

FORSYTHIA OVATA Nakai [no voucher found; reported from Rhode Island]

GERANIUM AEQUALE (Babington) Aedo [no vouchers of wild occurrence found; reported from Barnstable and Norfolk Counties, Massachusetts, and Chittenden County, Vermont]

GILIA CAPITATA Sims subsp. *CAPITATA* [no voucher of wild occurrence found; reported from Caledonia County, Vermont]

GLANDULARIA CANADENSIS (Linnaeus) Small (*VERBENA CANADENSIS* (Linnaeus Britton)) [no voucher of wild occurrence found; reported from New Haven County, Connecticut]

GLANDULARIA × *HYBRIDA* (Groenland & Rümpler) G.L. Nesom & Pruski [no voucher of wild occurrence found; reported from Nantucket County, Massachusetts]

HYDRANGEA CINEREA Small (*H. ARBORESCENS* Linnaeus var. *DEAMII* St. John) [no voucher of wild occurrence found; reported from Essex County, Massachusetts]

KOELREUTERIA PANICULATA Lamarck [no voucher of wild occurrence found; reported from various counties in Connecticut and Massachusetts]

LAMIUM ALBUM Linnaeus [no voucher of wild occurrence found; reported from Cumberland and Kennebec Counties, Maine, and Essex and Middlesex Counties, Massachusetts]

LAPPULA CENCHRUSOIDES A. Nelson [no voucher found; reported from Connecticut and Massachusetts]

LAVANDULA ANGUSTIFOLIA Miller [no voucher of wild occurrence found; reported from Chittenden, Orleans and Windham Counties, Vermont]

LITHOSPERMUM LATIFOLIUM Michaux [no voucher of wild occurrence found; reported from Essex County, Massachusetts]

LYCOPUS ASPER Greene [no voucher of wild occurrence found; reported from Essex County, Massachusetts]

Lythrum lineare Linnaeus [no voucher found; reported from Fairfield County, Connecticut]

LYTHRUM VIRGATUM Linnaeus [report based on misidentified *L. SALICARIA*; reported from Norfolk County, Massachusetts]

MERTENSIA PANICULATA (Aiton) G. Don [no voucher found; reported from Fairfield County, Connecticut]

MONARDA FISTULOSA Linnaeus var. *RUBRA* A. Gray (*M. MEDIA* misapplied) [no voucher of wild occurrence found; reported from various counties in Connecticut, Maine, Massachusetts and New Hampshire]

MONARDA PUNCTATA Linnaeus var. *PUNCTATA* [no voucher of wild occurrence found; reported from Essex County, Massachusetts, and Chittenden County, Vermont]

MYOSOTIS DISCOLOR Persoon (*M. VERSICOLOR* (Persoon) Smith) [no voucher of wild occurrence found; reported from Worcester County, Massachusetts]

NAVARRETIA INTERTEXTA (Bentham) Hooker subsp. *PROPINQUA* (Suksdorf) A.G. Day [no voucher found; reported from Massachusetts]

Oenothera elata Kunth subsp. *hirsutissima* (A. Gray *ex* S. Watson) W. Dietrich [no voucher found; reported from southern New England]

OENOTHERA FILIFORMIS (Small) W.L. Wagner & Hoch [no voucher found; reported from Hartford County, Connecticut, and Plymouth County, Massachusetts]

ORIGANUM MAJORANA Linnaeus [no voucher of wild occurrence found; reported from Essex and Worcester Counties, Massachusetts]

OXALIS INTERMEDIA A. Richard [no voucher of wild occurrence found; reported from Essex County, Massachusetts]

PHACELIA CAMPANULARIA A. Gray subsp. *CAMPANULARIA* [no voucher found; reported from Suffolk County, Massachusetts]

PHACELIA LINEARIS (Pursh) Holzinger [no voucher of wild occurrence found; reported from Hartford County, Connecticut, and Hancock County, Maine]

PHACELIA PURSHII Buckley [no voucher of wild occurrence found; reported from Connecticut, and Providence County, Rhode Island]

PHACELIA TANACETIFOLIA Bentham [no voucher of wild occurrence found; reported from Hancock County (Mt. Desert Island), Maine, and Middlesex and Worcester Counties, Massachusetts]

PHACELIA VISCIDA (Bentham *ex* Lindley) Torrey [no voucher found; reported from Connecticut]

PHLOX DRUMMONDII Hooker subsp. *DRUMMONDII* [no voucher of wild occurrence found; reported from New London County, Connecticut]

PHLOX LATIFOLIA Michaux (*PHLOX OVATA* misapplied) [no voucher found; reported from Berkshire County, Massachusetts]

PLAGIOBOTHRYS HISPIDULUS (Greene) I.M. Johnston [no voucher found; reported from York County, Maine, and Middlesex County, Massachusetts. The voucher for the

Middlesex County, Massachusetts, report has been identified as *P. RETICULATUS* (Piper) I.M. Johnston.]

PLAGIOBOTHRYS TRACHYCARPUS (A. Gray) I.M. Johnston [no voucher of wild occurrence found; reported from Hampshire County, Massachusetts]

POLEMONIUM CUSPIDATUM Siebold & Zuccarini [no voucher found; reported from Aroostook County, Maine]

POLEMONIUM MICRANTHUM Bentham [no voucher of wild occurrence found; reported from Norfolk County, Massachusetts.]

PRUNELLA LACINIATA Linnaeus [no voucher of wild occurrence found; reported from Dukes County, Massachusetts]

RHAMNUS DAVURICA Pallas subsp. *NIPPONICA* (Makino) Kartesz & Gandhi [no voucher of wild occurrence found; reported from Worcester County, Massachusetts]

RHAMNUS UTILIS Decaisne [no voucher found; reported from Tolland County, Connecticut]

SELINUM CARVIFOLIA (Linnaeus) Linnaeus [no voucher found; reported from vacant lot in Suffolk County, Massachusetts]

SCUTELLARIA ALTISSIMA Linnaeus [no voucher of wild occurrence found; reported from Suffolk County, Massachusetts]

Scutellaria parvula Michaux var. *australis* Fassett [no voucher found; reported from southern Connecticut]

SIUM SISARUM Linnaeus [no voucher of wild occurrence found; reported from Washington County, Rhode Island]

STACHYS CLINGMANII Small [no voucher found; reported from Vermont]

STACHYS OFFICINALIS (Linnaeus) Trevisan [no voucher found; reported from Middlesex County, Massachusetts]

SYRINGA JOSIKAEA J. Jacquin *ex* Reichenbach [no voucher found; reported from Berkshire County, Massachusetts]

THYMUS VULGARIS Linnaeus [no voucher of wild occurrence found; reported from Essex County, Vermont]

TRIBULUS TERRESTRIS Linnaeus [no voucher found; reported in wool waste from Worcester County, Massachusetts]

TURGENIA LATIFOLIA (Linnaeus) Hoffmann [no voucher found; reported from Providence County, Rhode Island]

ANGIOSPERMAE (MAGNOLIOPHYTA) – ANGIOSPERMS

ACTINIDIACEAE

ACTINIDIA ARGUTA (Siebold & Zuccarini) Planchon *ex* Miquel—Hardy Kiwi (Figure 2). 2*n* = 116. Roadsides, woodland margins. From eastern Asia.

ANACARDIACEAE

COTINUS COGGYGRIA Scopoli—Smoketree (Figure 2). 2*n* = 30. Waste places. From Eurasia.

Rhus aromatica Aiton var. *aromatica*—Fragrant Sumac (Figure 2). 2*n* = ? Dry ledges, rocky woodlands, often in calcareous soil, thickets as an escape.

Rhus copallinum Linnaeus var. *copallinum*—Winged Sumac (Figure 2). 2*n* = ? Dry woodlands, openings and thickets, roadsides. [*R. copallinum* var. *latifolia* Engler]

Rhus glabra Linnaeus—Smooth Sumac Elder (Figure 2). 2*n* = 30. Dry fields, roadsides, woodland margins.

Rhus typhina Linnaeus—Staghorn Sumac (Figure 2). 2*n* = 30. Open, wooded slopes, woodland margins, fields, roadsides, in dry, rocky or gravelly soil. [*R. hirta* (Linnaeus) Sudworth - rejected name]

— *Rhus* hybrid —

Rhus × *pulvinata* Greene (*pro species*)—(Figure 2). [*R. glabra* Linnaeus × *R. typhina* Linnaeus; *R.* × *borealis* (Britton) Greene; *R. glabra* Linnaeus var. *borealis* Britton]

Toxicodendron radicans (Linnaeus) Kuntze subsp. *radicans*—Poison Ivy (Figure 2). 2*n* = 30. Roadsides, thickets, stone walls, fencerows, open woodlands, woodland margins, open sandy or rocky soil, often in disturbed sites. [*Rhus radicans* Linnaeus]

Toxicodendron radicans (Linnaeus) Kuntze subsp. *negundo* (Greene) Gillis—(Figure 2). 2*n* = 30. Rich woodlands. [*T. radicans* var. *negundo* (Greene) Reveal]

Toxicodendron rydbergii (Small *ex* Rydberg) Greene—Western Poison Ivy (Figure 3). 2*n* = 30. Woodlands, rocky slopes, roadsides. [*Rhus radicans* Linnaeus var. *rydbergii* (Small *ex* Rydberg) Rehder; *R. radicans* var. *vulgaris* (Michaux) de Candolle]

Toxicodendron vernix (Linnaeus) Kuntze—Poison Sumac (Figure 3). 2*n* = 30. Swamps, wetland margins. [*Rhus vernix* Linnaeus]

— *Toxicodendron* hybrid —

Toxicodendron radicans (Linnaeus) Kuntze × *T. rydbergii* (Small *ex* Rydberg) Greene—(Figure 3).

APIACEAE

AEGOPODIUM PODAGRARIA Linnaeus—Goutweed (Figure 3). $2n = 22, 42, 44$. Roadsides, waste places, open woodlands, often in moist shade. From Eurasia.

AETHUSA CYNAPIUM Linnaeus—Fool's-parsley (Figure 3). $2n = 20$. Roadsides, waste places. From Eurasia.

ANETHUM GRAVEOLENS Linnaeus—Dill (Figure 3). $2n = 22$. Roadsides, waste places. Cultivated worldwide, probably from southern Asia.

Angelica atropurpurea Linnaeus—Alexanders (Figure 3). $2n = 22$. Brook and river margins, meadows, rich thickets, swamps, alluvial soil, roadside ditches.

Angelica lucida Linnaeus—Seacoast Angelica (Figure 3). $2n = ?$ Sea beach margins, fields by coastal beaches, rocks along coast. [*Coelopleurum lucidum* (Linnaeus) Fernald]

Angelica venenosa (J. Greenway) Fernald—Hairy Angelica (Figure 3). $2n = 22$. Woodlands, fields, thickets, openings, in dry soil.

ANTHRISCUS CEREFOLIUM (Linnaeus) Hoffman—Garden Chervil (Figure 4). $2n = 18$. Roadsides, waste places. From Eurasia.

ANTHRISCUS SYLVESTRIS (Linnaeus) Hoffman—Wild Chervil (Figure 4). $2n = 16$. Fields, waste places, roadsides. From Eurasia, northern and central Africa.

APIUM GRAVEOLENS Linnaeus var. *DULCE* (Miller) de Candolle—Celery (Figure 4). $2n = 22$. Waste places. From Eurasia.

BIFORA RADIANS M. von Bieberstein—Wild Bishop (Figure 4). $2n = 20$. Waste places. From Eurasia.

BUPLEURUM LANCIFOLIUM Hornemann—(Figure 4). $2n = 16$. Roadsides, waste places. From the Mediterranean region.

BUPLEURUM ROTUNDIFOLIUM Linnaeus—Thoroughwax (Figure 4). $2n = 16$. Roadsides, fields. From Eurasia, northwestern Africa.

CARUM CARVI Linnaeus—Caraway (Figure 4). $2n = 20$. Fields, roadsides, waste places. From Eurasia, northwestern Africa.

Cicuta bulbifera Linnaeus—(Figure 4). $2n = 22$. Swamps, marshes, shores, wet thickets.

Cicuta maculata Linnaeus var. *maculata*—Spotted Cowbane (Figure 4). $2n = 22$. Swamps, marshes, shores, meadows, low thickets, ditches.

Conioselinum chinense (Linnaeus) Britton, Sterns, & Poggenburg—Hemlock-parsley (Figure 5). $2n = 44$. River shores, swamps, wet woodlands, meadows, damp thickets.

CONIUM MACULATUM Linnaeus—Poison Hemlock (Figure 5). $2n = 22$. Waste places, roadsides. From Eurasia, northern Africa.

CORIANDRUM SATIVUM Linnaeus—Coriander (Figure 5). $2n = 22$. Waste places, sandy seashores. Probably from the Mediterranean region.

Cryptotaenia canadensis (Linnaeus) de Candolle—Honewort (Figure 5). $2n = 22$. Rich woodlands and thickets.

DAUCUS CAROTA Linnaeus—Queen Anne's-lace (Figure 5). $2n = 18$. Dry fields, waste places, roadsides. From Eurasia, northwestern Africa

ERYNGIUM AMETHYSTINUM Linnaeus—(Figure 5). $2n = 14$. Waste places, fields. From eastern Mediterranean region.

ERYNGIUM PLANUM Linnaeus—Blue Eryngo (Figure 5). $2n = 16$. Fields, waste places, roadsides. From Eurasia.

ERYNGIUM YUCCIFOLIUM Michaux var. *YUCCIFOLIUM*—Rattlesnake-master (Figure 5). $2n = 96$. Sandy fields, other open, sandy ground. From farther south and west.

FALCARIA VULGARIS Bernhardi—Sickleweed (Figure 5). $2n = 22$. Dry, open, calcareous knoll. From Eurasia.

FOENICULUM VULGARE Miller—Fennel (Figure 6). $2n = 22$. Waste places, dry fields, roadsides. From Eurasia, northern Africa.

HERACLEUM MANTEGAZZIANUM Sommier & Levier—Giant Hogweed (Figure 6). $2n = 22$. Roadsides, woodland clearings, field and woodland margins. From the Caucasus region.

Heracleum sphondylium Linnaeus subsp. *montanum* (Schleicher *ex* Gaudin) Briquet—Cow-parsnip (Figure 6). $2n = 22$. Moist, rich ground. [*H. lanatum* Michaux; *H. maximum* W. Bartram]

HERACLEUM SPHONDYLIUM Linnaeus subsp. *SIBIRICUM* (Linnaeus) Simonkai—Hogweed (Figure 6). $2n = 22$. Fields, roadsides, waste areas. From Eurasia. [*H. SPHONDYLIUM* var. *ANGUSTIFOLIUM* Jacquin]

LEVISTICUM OFFICINALE W.D.J. Koch—Lovage (Figure 6). $2n = 22$. Roadsides. From western Asia.

Ligusticum scoticum Linnaeus subsp. *scoticum*—Scots Lovage (Figure 6). $2n = 22$. Salt marsh margins, sandy or rocky seashores.

Lilaeopsis chinensis (Linnaeus) Kuntze—(Figure 6). $2n = 22$. Muddy tidal shores, salt marshes.

MYRRHIS ODORATA (Linnaeus) Scopoli—Garden Myrrh (Figure 6). $2n = 22$. Roadsides. From Europe.

Osmorhiza berteroi de Candolle—Mountain Sweet Cicely (Figure 6). $2n = 22$. Rich woodlands. [*O. chilensis* Hooker & Arnott]

Osmorhiza claytonii (Michaux) C.B. Clarke—Hairy Sweet Cicely (Figure 7). $2n = 22$. Rich woodlands.

Osmorhiza depauperata Philippi—(Figure 7). $2n = 22$. Moist, deciduous woodlands. [*O. obtusa* (J.M. Coulter & Rose) Fernald]

Osmorhiza longistylis (Torrey) de Candolle—Anise-root (Figure 7). $2n = 22$. Rich, moist woodlands. [*O. longistylis* var. *brachycoma* S.F. Blake; *O. longistylis* var. *villicaulis* Fernald]

PASTINACA SATIVA Linnaeus—Parsnip (Figure 7). $2n = 22$. Roadsides, waste places, fields. From Eurasia.

PETROSELINUM CRISPUM (Miller) Fuss—Common Parsley (Figure 7). $2n = 22$. Waste places, fields. From the Mediterranean region.

PEUCEDANUM PALUSTRE (Linnaeus) Moench—Milk-parsley (Figure 7). $2n = 22$. Meadows, damp fields, swampy thickets. From Eurasia.

PIMPINELLA ANISUM Linnaeus—Anise (Figure 7). $2n = 18, 20$. Waste places. From eastern Mediterranean region, southwestern Asia.

PIMPINELLA MAJOR (Linnaeus) Hudson—(Figure 7). $2n = 18, 20$. Moist roadsides. From Europe.

PIMPINELLA SAXIFRAGA Linnaeus subsp. *SAXIFRAGA*—Burnet-saxifrage (Figure 7). $2n = 40$. Cemeteries, fields, roadsides, waste places. From Eurasia.

Ptilimnium capillaceum (Michaux) Rafinesque—(Figure 8). $2n = 14, 16, 28$. Salt marshes.

Sanicula canadensis Linnaeus var. *canadensis*—(Figure 8). $2n = 16$. Rich woodlands.

Sanicula canadensis Linnaeus var. *grandis* Fernald—(Figure 8). $2n = ?$ Rich woodlands.

Sanicula marilandica Linnaeus—Black Snakeroot (Figure 8). $2n = 16$. Open woodlands, thickets, often in dry, rich, rocky soil.

Sanicula odorata (Rafinesque) K.M. Pryer & L.R. Phillippe—(Figure 8). $2n = ?$ Rich woodlands. [*S. gregaria* E.P. Bicknell]

Sanicula trifoliata E.P. Bicknell—(Figure 8). $2n = ?$ Rich woodlands.

SCANDIX PECTEN-VENERIS Linnaeus—Shepherd's-needle (Figure 8). $2n = 26$. Waste places. From Eurasia, northern Africa.

Sium carsonii Durand *ex* A. Gray—(Figure 8). $2n = ?$ Brooks, shallow water of streams.

Sium suave Walter—Water-parsnip (Figure 8). $2n = 12$. Swamps, shores, meadows, wet thickets.

Taenidia integerrima (Linnaeus) Drude—Yellow Pimpernel (Figure 9). $2n = 22$. Dry, open, rocky woodlands near shores.

Thaspium trifoliatum (Linnaeus) A. Gray var. *trifoliatum*—Purple Meadow-parsnip (Figure 9). $2n$ = 22. Rich woodlands.

TORILIS JAPONICA (Houttuyn) de Candolle—(Figure 9). $2n$ = 16. Woodland margins, roadsides, waste places. From Eurasia.

TORILIS LEPTOPHYLLA (Linnaeus) Reichenbach (son)—(Figure 9). $2n$ = 12. Waste places. From Eurasia, northern Africa.

Zizia aptera (A. Gray) Fernald—(Figure 9). $2n$ = 22. Dry, open woodlands, openings.

Zizia aurea (Linnaeus) W.D.J. Koch—Golden Alexanders (Figure 9). $2n$ = 22. Shores, meadows, damp thickets, wet woodlands, shaded roadsides.

ARALIACEAE

ARALIA ELATA (Miquel) Seemann—Japanese Angelica-tree (Figure 9). $2n$ = 24. Roadsides, thickets, streambanks, field margins. From eastern Asia.

Aralia hispida Ventenat—Bristly Sarsaparilla (Figure 9). $2n$ = 24. Roadsides, sandy or rocky open woodlands and clearings, in dry soil.

Aralia nudicaulis Linnaeus—Wild Sarsaparilla (Figure 9). $2n$ = 24, 48. Woodlands.

Aralia racemosa Linnaeus subsp. *racemosa*—Spikenard (Figure 10). $2n$ = 24. Woodlands, thickets, woodland margins, in rich soil.

ARALIA SPINOSA Linnaeus—Hercules'-club (Figure 10). $2n$ = 24. Thickets, roadsides, woodland margins.

ELEUTHEROCOCCUS SIEBOLDIANUS (Makino) Koidzumi—(Figure 10). $2n$ = 48. Roadsides, waste places, woodlands near waste places. From Japan. [*E. PENTAPHYLLUS* (Siebold & Zuccarini) Nakai; *ACANTHOPANAX SIEBOLDIANUS* Makino]

HEDERA HELIX Linnaeus—English Ivy (Figure 10). $2n$ = 48. Roadsides, disturbed woodlands. From Eurasia, northwestern Africa.

Hydrocotyle americana Linnaeus—Marsh Pennywort (Figure 10). $2n$ = 60. Damp woodlands and thickets, swamps, meadows, wet fields, stream margins, freshwater shores, wet ditches.

Hydrocotyle umbellata Linnaeus—Water Pennywort (Figure 10). $2n$ = ? Pond shores.

Hydrocotyle verticillata Thunberg var. *verticillata*—Whorled Pennywort (Figure 10). $2n$ = ? Pond shores.

Hydrocotyle verticillata Thunberg var. *triradiata* (A. Richard) Fernald—(Figure 10). $2n$ = ? Damp soils. [*H. prolifera* Kellogg]

KALOPANAX SEPTEMLOBUS (Thunberg) Koidzumi—Castor Aralia (Figure 10). $2n = 48$. Moist or rich woodlands, woodland margins. From eastern Asia. [*K. PICTUS* (Thunberg) Nakai]

Panax quinquefolius Linnaeus—Ginseng (Figure 11). $2n = 44, 48$. Rich woodlands.

Panax trifolius Linnaeus—Dwarf Ginseng (Figure 11). $2n = 24$. Rich, moist woodlands.

BALSAMINACEAE

IMPATIENS BALSAMINA Linnaeus—Garden Balsam (Figure 11). $2n = 14$. Waste places, beaches. From southern Asia.

Impatiens capensis Meerburgh—Spotted Touch-me-not (Figure 11). $2n = 20$. Swamps, springy places, brooksides, wet, roadside ditches, moist, shady soil.

IMPATIENS GLANDULIFERA Royle—(Figure 11). $2n = 18, 20$. Waste places, roadsides, in rich soil. From Indian subcontinent.

Impatiens pallida Nuttall—Pale Touch-me-not (Figure 11). $2n = 20, 30$. Springy places, wet, deciduous woodlands, moist, shady, chiefly calcareous soil.

BORAGINACEAE

AMSINCKIA EASTWOODIAE J.F. Macbride—(Figure 11). $2n = ?$ Moist ledges. From California. [*A. INTERMEDIA* Fischer & C.A. Meyer var. *EASTWOODIAE* (J.F. Macbride) Jepson & Hoover]

AMSINCKIA INTERMEDIA Fischer & C.A. Meyer—Common Fiddleneck (Figure 11). $2n = 15, 34$. Wool waste, roadsides, grassy hills. From western North America. [*A. MENZIESII* (Lehmann) A. Nelson & J.F. Macbride var. *INTERMEDIA* (Fischer & C.A. Meyer) Ganders]

AMSINCKIA LYCOPSOIDES Lehmann—Bugloss Fiddleneck (Figure 11). $2n = 30$. Railroads, waste places. From western North America. [*A. BARBATA* Greene]

AMSINCKIA MENZIESII (Lehmann) A. Nelson & J.F. Macbride—Rancher's Fiddleneck (Figure 12). $2n = ?$ Wool waste, roadsides. From western North America

ANCHUSA ARVENSIS (Linnaeus) M. von Bieberstein—Small Bugloss (Figure 12). $2n = 48$. Sandy fields, waste places, railroads, wool waste. From Europe. [*LYCOPSIS ARVENSIS* Linnaeus]

ANCHUSA AZUREA Miller—Italian Bugloss (Figure 12). $2n = 32$. Waste places, field margins, roadsides. From Eurasia, northern Africa.

ANCHUSA LEPTOPHYLLA Roemer & Schultes subsp. *LEPTOPHYLLA*—(Figure 12). $2n = 16, 32$. Waste places. From Eurasia.

ANCHUSA OFFICINALIS Linnaeus—Common Bugloss (Figure 12). $2n = 16$. Waste places, roadsides. From Europe.

ASPERUGO PROCUMBENS Linnaeus—Madwort (Figure 12). $2n = 48$. Waste places, streambanks. From Eurasia.

BORAGO OFFICINALIS Linnaeus—Borage (Figure 12). $2n = 16$. Waste places, fields. From Eurasia, northwestern Africa.

BUGLOSSOIDES ARVENSIS (Linnaeus) I.M. Johnston—Corn Gromwell (Figure 12). $2n = 28, 42$. Waste places, roadsides, railroads, sandy fields. From Eurasia, northern Africa. [*LITHOSPERMUM ARVENSE* Linnaeus]

CRYPTANTHA AMBIGUA (A. Gray) Greene—(Figure 12). $2n = ?$ Wool waste. From western North America.

CRYPTANTHA INTERMEDIA (A. Gray) Greene—(Figure 13). $2n = 44$. Wool waste. From western North America.

CYNOGLOSSUM AMABILE Stapf & J.R. Drummond—Chinese Hound's-tongue (Figure 13). $2n = 24$. Roadsides, waste places. From China.

CYNOGLOSSUM MICROGLOCHIN Bentham—(Figure 13). $2n = ?$ Waste places. From central and southern Asia.

CYNOGLOSSUM OFFICINALE Linnaeus—Common Hound's-tongue (Figure 13). $2n = 24$. Dry fields, roadsides, waste places. From Eurasia.

Cynoglossum virginianum Linnaeus var. *virginianum*—Wild Comfrey (Figure 13). $2n = ?$ Open, deciduous or mixed woodlands.

Cynoglossum virginianum Linnaeus var. *boreale* (Fernald) Cooperrider—Northern Wild Comfrey (Figure 13). $2n = ?$ Rich, open woodlands. [*C. boreale* Fernald]

CYNOGLOTTIS BARRELIERI (Allioni) Vural & Kit Tan—False Alkanet (Figure 13). $2n = 36$. Gravelly roadsides. From Europe. [*ANCHUSA BARRELIERI* Vitman]

ECHIUM CRETICUM Linnaeus—(Figure 13). $2n = ?$ Waste places. From the Mediterranean region. [*E. AUSTRALE* Lamarck]

ECHIUM PLANTAGINEUM Linnaeus—Paterson's-curse (Figure 13). $2n = 16$. Waste places. From Eurasia, northern Africa. [*E. VIOLACEUM* misapplied]

ECHIUM PUSTULATUM Smith—(Figure 14). $2n = ?$ Fields. From Europe. [*E. VULGARE* Linnaeus var. *PUSTULATUM* (Smith) Coincy]

ECHIUM VULGARE Linnaeus—Blueweed (Figure 14). $2n = 32$. Waste places, railroads, dry fields, roadsides. From Eurasia.

Hackelia deflexa (Wahlenberg) Opiz var. *americana* (A. Gray) Fernald & I.M. Johnston—(Figure 14). $2n = ?$ Calcareous rocky woodlands or talus, roadsides. [*H. americana* (A. Gray) Fernald]

Hackelia virginiana (Linnaeus) I.M. Johnston—(Figure 14). $2n = 24$. Rich, open, deciduous woodlands and thickets, roadsides.

HELIOTROPIUM AMPLEXICAULE Vahl—(Figure 14). $2n = 26, 28$. Waste places. From South America.

HELIOTROPIUM CURASSAVICUM Linnaeus var. *CURASSAVICUM*—Seaside Heliotrope (Figure 14). $2n = 26, 28$. Sandy, saline soil. From southeastern North America, Central and South America.

HELIOTROPIUM EUROPAEUM Linnaeus—European Heliotrope (Figure 14). $2n = 24, 32, 48$. Waste places, wool waste. From Eurasia, northern Africa, Australia.

HELIOTROPIUM INDICUM Linnaeus—Turnsole (Figure 14). $2n = 22, 24$. Waste places. From South America.

LAPPULA OCCIDENTALIS (S. Watson) Greene var. *OCCIDENTALIS*—Western Stickseed (Figure 14). $2n = 48$. Waste places, fields, wool waste. From western North America. [*L. REDOWSKI* misapplied]

LAPPULA SQUARROSA (Retzius) Dumortier—Bur Forget-me-not (Figure 15). $2n = 48$. Roadsides, waste places, fields. From Eurasia. [*L. ECHINATA* Gilibert, invalid name]

LITHOSPERMUM CANESCENS (Michaux) Lehmann—Hoary Puccoon (Figure 15). $2n = 14$. Beaches. From farther west and south.

LITHOSPERMUM OCCIDENTALE (Mackenzie) Weakley, Witsell, & D. Estes—(Figure 15). $2n = ?$ Waste places. From farther west. [*ONOSMODIUM BEJARIENSE* A. de Candolle var. *OCCIDENTALE* (Mackenzie) B.L. Turner; *O. MOLLE* Michaux var. *OCCIDENTALE* (Mackenzie) I.M. Johnston; *O. OCCIDENTALE* Mackenzie]

LITHOSPERMUM OFFICINALE Linnaeus—European Gromwell (Figure 15). $2n = 28$. Dry fields, roadsides, open places, waste places. From Eurasia.

Lithospermum virginianum Linnaeus—Wild Job's-tears (Figure 15). $2n = ?$ Dry, sandy soil. [*Onosmodium virginianum* (Linnaeus) A. de Candolle]

Mertensia maritima (Linnaeus) Gray subsp. *tenella* (Th. Fries) Elven & Skarpaas—(Figure 15). $2n = 24$. Sea beaches, often gravelly.

MERTENSIA VIRGINICA (Linnaeus) Persoon *ex* Link—Virginia Cowslip (Figure 15). $2n = 24$. Waste places. From farther west and south.

MYOSOTIS ARVENSIS (Linnaeus) Hill—(Figure 15). $2n = 48, 52, 66$. Roadsides, waste places, fields. From Eurasia, northwestern Africa.

Myosotis laxa Lehmann—Smaller Forget-me-not (Figure 15). $2n = ?$ Springs, muddy or gravelly shores.

MYOSOTIS SCORPIOIDES Linnaeus—True Forget-me-not (Figure 16). 2*n* = 66. Springs, muddy shores, quiet water, wet ditches, swampy meadows, and other wet ground. From Eurasia.

MYOSOTIS STRICTA Link *ex* Roemer & Schultes—(Figure 16). 2*n* = 24, 36, 48. Old fields, roadsides, waste places, often in rocky soil. From Eurasia, northwestern Africa. [*M. MICRANTHA* misapplied]

MYOSOTIS SYLVATICA Hoffmann—Garden Forget-me-not (Figure 16). 2*n* = 18. Roadsides, waste places. From Eurasia.

Myosotis verna Nuttall—Early Scorpion-grass (Figure 16). 2*n* = ? Dry, rocky woodlands, ledges, open banks.

NONEA ROSEA (M. von Bieberstein) Link—(Figure 16). 2*n* = ? Waste places. From southeastern Europe.

PENTAGLOTTIS SEMPERVIRENS (Linnaeus) Tausch *ex* L.H. Bailey—Green Alkanet (Figure 16). 2*n* = 22. Copse near beach. From southwestern Europe.

PLAGIOBOTHRYS RETICULATUS (Piper) I.M. Johnston—(Figure 16). 2*n* = ? Wool waste. From western North America.

PULMONARIA SACCHARATA Miller—Bethlehem Sage (Figure 16). 2*n* = 22, 26, 27, 28. Roadsides. Probably from Europe.

SYMPHYTUM ASPERUM Lepechin—Prickly Comfrey (Figure 16). 2*n* = 32, (45). Roadsides, waste places. From the Caucasus region.

SYMPHYTUM OFFICINALE Linnaeus—Common Comfrey (Figure 17). 2*n* = 24, 40, 48, 56. Roadsides, waste places. From Eurasia.

SYMPHYTUM TUBEROSUM Linnaeus—(Figure 17). 2*n* = 32, 64, 96, (120), (144). Ditches, fields. From Europe.

— *Symphytum* hybrid —

SYMPHYTUM × *UPLANDICUM* Nyman (*pro species*)—(Figure 17). [*S. ASPERUM* Lepechin × *S. OFFICINALE* Linnaeus]

BUXACEAE

PACHYSANDRA TERMINALIS Siebold & Zuccarini—Japanese Pachysandra (Figure 17). 2*n* = 24, 48. Roadsides, railroads, waste places, woodland margins, open woodlands. From eastern Asia.

CELASTRACEAE

CELASTRUS ORBICULATUS Thunberg—Asian Bittersweet (Figure 17). $2n = 46$. Roadsides, thickets, woodland margins, open woodlands. From eastern Asia.

Celastrus scandens Linnaeus—American Bittersweet (Figure 17). $2n = 46$. River thickets, roadsides, woodland margins, rocky, deciduous woodlands, usually in rich soil.

EUONYMUS ALATUS (Thunberg) Siebold—Winged Euonymus (Figure 17). $2n$ = ca. 40. Roadsides, woodlands, streambanks, thickets, clearings. From eastern Asia.

EUONYMUS ATROPURPUREUS Jacquin var. *ATROPURPUREUS*—Wahoo (Figure 17). $2n = ?$ Roadsides, thickets, railroads, woodlands. From farther south and west.

EUONYMUS EUROPAEUS Linnaeus—European Spindle-tree (Figure 17). $2n = 64$. Woodlands, roadsides, waste places. From Eurasia.

EUONYMUS FORTUNEI (Turczaninow) Handel-Mazzetti var. *FORTUNEI*—Winter-creeper (Figure 18). $2n = ?$ Thickets, roadsides, woodland margins, waste places. From southern and eastern Asia.

EUONYMUS FORTUNEI (Turczaninow) Handel-Mazzetti var. *RADICANS* (Siebold *ex* Miquel) Rehder—Winter-creeper (Figure 18). $2n = ?$ Roadsides, railroads, open, rocky hillsides, woodlands. From eastern Asia.

Parnassia glauca Rafinesque—(Figure 18). $2n = 36$. Streambanks, boggy spots, fens, meadows, in wet ,calcareous soil.

COMANDRACEAE

Comandra umbellata (Linnaeus) Nuttall subsp. *umbellata*—Bastard Toadflax (Figure 18). $2n = 26$. Dry, usually sterile, open woodlands and clearings. [*C. richardsiana* Fernald]

Geocaulon lividum (Richardson) Fernald—(Figure 18). $2n = 26$. *Sphagnum* bogs, often at high altitudes, sphagnous openings, occasionally coastal peatlands.

CORNACEAE

Cornus alternifolia Linnaeus (son)—Pagoda Dogwood (Figure 18). $2n = 20$. Rich, dry, open woodlands, thickets.

Cornus amomum Miller—Silky Dogwood (Figure 18). $2n = 22$. Wet thickets, shores, meadows, swamps, marshes.

Cornus canadensis Linnaeus—Bunchberry (Figure 18). $2n = 22, 44$. Acidic, usually moist, woodlands, swamps.

Cornus florida Linnaeus—Flowering Dogwood (Figure 18). $2n = 22$. Rich, acidic woodlands.

Cornus obliqua Rafinesque—Pale Dogwood (Figure 19). 2*n* = 22. Wet thickets, swamps, woodlands, roadsides. [*C. amomum* Miller var. *schuetzeana* (C.A. Meyer) Rickett]

Cornus racemosa Lamarck—Gray Dogwood (Figure 19). 2*n* = 22. Thickets, woodlands, roadsides, streambanks, swamps.

Cornus rugosa Lamarck—Round-leaved Dogwood (Figure 19). 2*n* = 22. Woodlands, thickets, rocky slopes, usually in rich soil.

CORNUS SANGUINEA Linnaeus—Blood-twig Dogwood (Figure 19). 2*n* = 22. Railroads, damp thickets. From Eurasia.

Cornus stolonifera Michaux—Red-osier Dogwood (Figure 19). 2*n* = 22. Streambanks, wet thickets, shores, wet or swampy woodlands, meadows, wet roadsides. [*C. sericea* Linnaeus, ambiguous name]

— *Cornus* hybrids —

Cornus × *arnoldiana* Rehder—(Figure 19). [*C. amomum* Miller × *C. racemosa* Lamarck]

Cornus × *slavinii* Rehder—(Figure 19). [*C. rugosa* Lamarck × *C. stolonifera* Michaux]

ELAEAGNACEAE

ELAEAGNUS ANGUSTIFOLIA Linnaeus—Russian Olive (Figure 19). 2*n* = 28. Roadsides, waste places, streambanks. From Eurasia.

ELAEAGNUS MULTIFLORA Thunberg—Cherry Elaeagnus (Figure 19). 2*n* = ? Roadsides, dry woodlands, brook banks. From eastern Asia.

ELAEAGNUS UMBELLATA Thunberg var. *PARVIFOLIA* (Wallich *ex* Royle) C.K. Schneider—Autumn Olive (Figure 20). 2*n* = ? Thickets, roadsides, railroads, fields, woodland margins, brook margins, waste places. From Asia.

Shepherdia canadensis (Linnaeus) Nuttall—Soapberry (Figure 20). 2*n* = 22. Calcareous ledges and rocky outcrops along shores of rivers and lakes.

ELATINACEAE

Elatine americana (Pursh) Arnott—(Figure 20). 2*n* = 70-72. Muddy shores of ponds and streams, often tidal. [*E. triandra* Schkuhr var. *americana* Fassett]

Elatine minima (Nuttall) Fischer & C.A. Meyer—(Figure 20). 2*n* = ? Pond and lake shores, usually muddy, often in shallow water.

ELATINE TRIANDRA Schkuhr—(Figure 20). 2*n* = ? Pond and lake shores, quiet water of streams. From Eurasia.

EUPHORBIACEAE

Acalypha gracilens A. Gray—(Figure 20). $2n = 40$. Dry fields, sandy thickets, roadsides, waste places.

Acalypha rhomboidea Rafinesque—(Figure 20). $2n = ?$ Fields, roadsides, woodland margins, waste places.

Acalypha virginica Linnaeus—(Figure 20). $2n = 40$. Waste places, roadsides, fields, open woodlands, in dry soils.

CROTON CAPITATUS Michaux—Hogwort (Figure 20). $2n = 20$. Waste places. From farther west and south.

CROTON GLANDULOSUS Linnaeus var. *SEPTENTRIONALIS* Müller Argoviensis—(Figure 21). $2n = ?$ Roadsides. From farther south and west.

CROTON MICHAUXII G.L. Webster var. *ELLIPTICA* (Willdenow) B.W. van Ee & P.E. Berry—(Figure 21). $2n = ?$ Old fields, dry, sandy wastes. From farther south and west. [*C. WILLDENOWII* G.L. Webster; *CROTONOPSIS ELLIPTICA* Willdenow]

CROTON TEXENSIS (Klotzsch) Müller Argoviensis—(Figure 21). $2n = ?$ Waste places. From farther west.

EUPHORBIA COROLLATA Linnaeus—Flowering Spurge (Figure 21). $2n = 28$. Fields, dry, open woodlands, roadsides. From farther south and west.

EUPHORBIA CYPARISSIAS Linnaeus—Cypress Spurge (Figure 21). $2n = 20, 40$. Roadsides, waste places, old fields, cemeteries. From Eurasia.

EUPHORBIA DAVIDII Subils—(Figure 21). $2n = ?$ Railroads. From farther west. [*E. DENTATA* misapplied]

EUPHORBIA DENTATA Michaux—(Figure 21). $2n = 28, 56$. Waste places, roadsides, railroads, sandy beaches, cemeteries. From farther south and west. [Note: Many or all of the New England records under this name might be *EUPHORBIA DAVIDII* as they have not yet been reviewed for this common error.]

EUPHORBIA DULCIS Linnaeus—Sweet Spurge (Figure 21). $2n = 12, 18, 24, 28$. Thicket in oak woodlands. From Europe.

EUPHORBIA ESULA Linnaeus—Wolf's-milk (Figure 21). $2n = 20, 60, 64$. Roadsides, waste places, fields. From Eurasia. [*E. ESULA* var. *URALENSIS* (Fischer *ex* Link) Dorn; *E. VIRGATA* Waldstein & Kitaibel]

Euphorbia glyptosperma Engelmann—(Figure 22). $2n = 22$. Roadsides, railroads, dry, open soil.

EUPHORBIA HELIOSCOPIA Linnaeus—Wartweed (Figure 22). $2n = 42$. Roadsides, waste places, fields, dry, open soil. From Eurasia, northern Africa.

EUPHORBIA LATHYRIS Linnaeus—Caper Spurge (Figure 22). 2*n* = 20. Fields, roadsides, waste places. From Mediterranean Europe.

Euphorbia maculata Linnaeus—Milk-purslane (Figure 22). 2*n* = 12, 28, 42, 56. Railroads, waste places, roadsides, dry, open soil. [*E. supina* Rafinesque]

EUPHORBIA MARGINATA Pursh—Snow-on-the-mountain (Figure 22). 2*n* = 56. Waste places. From farther west.

EUPHORBIA MESEMBRIANTHEMIFOLIA Jacquin—(Figure 22). 2*n* = ? Woodlands. From Florida, Caribbean region.

Euphorbia nutans Lagasca—Eyebane (Figure 22). 2*n* = 12. Waste places, railroads, roadsides, fields, dry, open soil. [*E. maculata* misapplied]

EUPHORBIA PEPLUS Linnaeus—Petty Spurge (Figure 22). 2*n* = 16. Waste places. From Eurasia, northern Africa.

EUPHORBIA PLATYPHYLLOS Linnaeus—(Figure 22). 2*n* = (14), 28, 30. Waste places, meadows, lake shores. From the Mediterranean region.

Euphorbia polygonifolia Linnaeus—Seaside Spurge (Figure 23). 2*n* = 26. Sand dunes, sea beaches.

EUPHORBIA PROSTRATA Aiton—(Figure 23). 2*n* = 18. Cotton waste. From farther west and south, Mexico, Central and South America, Caribbean region.

Euphorbia vermiculata Rafinesque—(Figure 23). 2*n* = 16. Railroads, roadsides, waste places, fields, dry, sandy soil.

— *Euphorbia* hybrid —

EUPHORBIA × *PSEUDOESULA* Schur (*pro species*)—(Figure 23). [*E. CYPARISSIAS* Linnaeus × *E. ESULA* Linnaeus]

MERCURIALIS ANNUA Linnaeus—Herb Mercury (Figure 23). 2*n* = 16, 32, 48, 64. Waste places. From Eurasia, northern Africa.

RICINUS COMMUNIS Linnaeus—Castor-bean (Figure 23). 2*n* = 20. Waste places, railroads. Probably from Africa.

GERANIACEAE

ERODIUM BOTRYS (Cavanilles) Bertoloni—(Figure 23). 2*n* = 40, (60). Wool waste. From Eurasia, northwestern Africa.

ERODIUM BRACHYCARPUM (Godron) Thellung—(Figure 23). 2*n* = 40. Wool waste. From southern Europe.

ERODIUM CICONIUM (Linnaeus) L'Héritier—(Figure 23). $2n = 18, 20$. Wool waste, waste places. From Eurasia, northern Africa.

ERODIUM CICUTARIUM (Linnaeus) L'Héritier subsp. *CICUTARIUM*—Alfilaria (Figure 24). $2n = 40$. Wool waste, waste places, fields, roadsides. From Eurasia, northern Africa.

ERODIUM CYGNORUM Nees—Australian Stork's-bill (Figure 24). $2n = 20, 40$. Wool waste. From Australia.

ERODIUM MALACOIDES (Linnaeus) L'Héritier—(Figure 24). $2n = 40$. Wool waste. From Eurasia, northern Africa.

ERODIUM MOSCHATUM (Linnaeus) L'Héritier—(Figure 24). $2n = 20$. Wool waste, waste places, railroads. From Eurasia, northern Africa. [*E. MOSCHATUM* var. *PRAECOX* Lange]

ERODIUM STEPHANIANUM Willdenow—(Figure 24). $2n = 16$. Wool waste. From Asia.

Geranium bicknellii Britton—(Figure 24). $2n = 52$. Roadsides, waste places, dry ledges, open woodlands, clearings, fields.

Geranium carolinianum Linnaeus var. *carolinianum*—(Figure 24). $2n = 52$. Waste places, roadsides, fields, rocky woodlands, dry, sandy soil. [*G. carolinianum* var. *confertiflorum* Fernald]

GERANIUM COLUMBINUM Linnaeus—Long-stalked Cranesbill (Figure 24). $2n = 18$. Woodland margins, dry, sandy, somewhat calcareous, old fields. From Eurasia, northwestern Africa.

GERANIUM DISSECTUM Linnaeus—(Figure 24). $2n = 22$. Waste places, roadsides. From Eurasia, northern Africa.

GERANIUM ERIANTHUM de Candolle—(Figure 25). $2n = 28$. Roadside ledges. From northwestern North America, northeastern Asia. [*G. PRATENSE* Linnaeus var. *ERIANTHUM* (de Candolle) B. Boivin]

Geranium maculatum Linnaeus—Wild Geranium (Figure 25). $2n = 52$. Thickets, meadows, roadsides, woodlands, clearings.

GERANIUM MOLLE Linnaeus—Dovesfoot Cranesbill (Figure 25). $2n = 26$. Waste places, fields, roadsides. From Eurasia, northern Africa.

GERANIUM PRATENSE Linnaeus—(Figure 25). $2n = 28$. Fields, meadows, roadsides. From Eurasia.

GERANIUM PUSILLUM Linnaeus—Small-flowered Cranesbill (Figure 25). $2n = 26$. Waste places, fields, roadsides. From Eurasia, northern Africa.

GERANIUM PYRENAICUM Burman (son)—(Figure 25). $2n = 26$. Waste places. From Eurasia, northwestern Africa.

Geranium robertianum Linnaeus—Herb-Robert (Figure 25). $2n = 64$. Rocky woodlands, ledges, coastal beaches, gravelly shores.

GERANIUM SANGUINEUM Linnaeus—Bloody Cranesbill (Figure 25). 2*n* = 84. Damp fields, clearings, railroad ballast, waste places, cemeteries. From Eurasia.

GERANIUM SIBIRICUM Linnaeus—Siberian Cranesbill (Figure 25). 2*n* = 28. Waste places, roadsides, fields. From Eurasia.

GERANIUM THUNBERGII Siebold *ex* Lindley & Paxton—(Figure 26). 2*n* = 28. Sandy, open area, open path by pond. From eastern Asia. [*G. NEPALENSE* Sweet var. *THUNBERGII* (Siebold *ex* Lindley & Paxton) Kudô]

HALORAGACEAE

Myriophyllum alterniflorum de Candolle—(Figure 26). 2*n* = 14. Quiet water of ponds, lakes and streams.

MYRIOPHYLLUM AQUATICUM (Vellozo) Verdcourt—Parrot's-feather (Figure 26). 2*n* = ? Quiet water of ponds and streams. From South America.

Myriophyllum farwellii Morong—(Figure 26). 2*n* = ? Quiet water of ponds and streams.

MYRIOPHYLLUM HETEROPHYLLUM Michaux—(Figure 26). 2*n* = ? Quiet water of ponds, lakes and streams. From farther south and west.

Myriophyllum humile (Rafinesque) Morong—(Figure 26). 2*n* = ? Quiet water of ponds, lakes and streams, shorelines of receding waters.

Myriophyllum pinnatum (Walter) Britton, Sterns & Poggenburg—(Figure 26). 2*n* = ? Peaty or muddy shores, shallow waters.

Myriophyllum sibiricum Komarov—Siberian Water-milfoil (Figure 26). 2*n* = ? Quiet waters of lakes, ponds, and streams, in circumneutral or calcareous water. [*M. exalbescens* Fernald]

MYRIOPHYLLUM SPICATUM Linnaeus—Eurasian Water-milfoil (Figure 26). 2*n* = 42. Quiet waters of lakes, ponds, and streams, in circumneutral or calcareous water. From Eurasia, northwestern Africa.

Myriophyllum tenellum Bigelow—(Figure 27). 2*n* = 14. Shallow water, or sandy or muddy shores, of of circumneutral or acidic ponds and lakes.

Myriophyllum verticillatum Linnaeus—(Figure 27). 2*n* = 28. Quiet water of ponds, lakes and streams. [*M. verticillatum* var. *pectinatum* Wallroth]

— *Myriophyllum* hybrids —

MYRIOPHYLLUM HETEROPHYLLUM Michaux × *M. LAXUM* Shuttleworth *ex* Chapman—(Figure 27).

MYRIOPHYLLUM HETEROPHYLLUM Michaux × *M. pinnatum* (Walter) Britton, Sterns & Poggenburg—(Figure 27).

Proserpinaca intermedia Mackenzie—(Figure 27). 2*n* = ? Shallow water and shores of acidic ponds and lakes.

Proserpinaca palustris Linnaeus var. *palustris*—(Figure 27). 2*n* = ? Shallow water and shores of acidic ponds and lakes.

Proserpinaca palustris Linnaeus var. *crebra* Fernald & Griscom—(Figure 27). 2*n* = ? Shallow water and shores of acidic ponds and lakes.

Proserpinaca pectinata Lamarck—(Figure 27). 2*n* = ? Sandy or peaty, acidic ponds, pools, or depressions, swamps.

HYDRANGEACEAE

DEUTZIA SCABRA Thunberg—(Figure 27). 2*n* = 26. Waste places, roadsides, cemeteries, thickets, woodlands, streambanks. From Japan.

HYDRANGEA ARBORESCENS Linnaeus—Wild Hydrangea (Figure 28). 2*n* = 36, 38. Roadsides, swamps, streambanks, thickets. From farther south and west.

HYDRANGEA PANICULATA Siebold—(Figure 28). 2*n* = (36), 72, (108). Swamps, damp woodlands, roadsides, streambanks. From eastern Asia.

HYDRANGEA QUERCIFOLIA W. Bartram—(Figure 28). 2*n* = ? Dry, open hillsides. From southeastern United States.

HYDRANGEA RADIATA Walter—Silverleaf Hydrangea (Figure 28). 2*n* = 36. Waste places. From southeastern United States. [*H. ARBORESCENS* Linnaeus subsp. *RADIATA* (Walter) E.M. McClintock]

PHILADELPHUS CORONARIUS Linnaeus—Sweet Mock-orange (Figure 28). 2*n* = 26. Woodlands, roadside thickets, woodland margins. From Eurasia. [*P. CAUCASICUS* Koehne]

PHILADELPHUS INCANUS Koehne—(Figure 28). 2*n* = ? Margins of rich woodlands. From China.

PHILADELPHUS INODORUS Linnaeus—(Figure 28). 2*n* = 26. Woodland margins, roadsides. From southeastern United States. [*P. INODORUS* var. *GRANDIFLORUS* (Willdenow) A. Gray]

PHILADELPHUS PUBESCENS Loiseleur—(Figure 28). 2*n* = 26. Waste places, streambanks, deciduous woodlands, thickets. From farther west and south. [*P. PUBESCENS* var. *VERRUCOSUS* (Schrader *ex* de Candolle) S.Y. Hu]

— *Philadelphus* hybrids —

PHILADELPHUS × *NIVALIS* Jacques—(Figure 28). [*P. CORONARIUS* Linnaeus × *P. PUBESCENS* Loiseleur]

PHILADELPHUS × *POLYANTHUS* Rehder—(Figure 29). [*P. CORONARIUS* Linnaeus × ?]

PHILADELPHUS × *VIRGINALIS* Rehder—(Figure 29). [unknown parentage]

HYDROPHYLLACEAE

ELLISIA NYCTELEA (Linnaeus) Linnaeus—Water-pod (Figure 29). 2*n* = 20. Fields. From farther west and south.

Hydrophyllum canadense Linnaeus—(Figure 29). 2*n* = 18. Damp, rich woodlands, mountain brooksides, rich humus at base of calcareous ledges.

Hydrophyllum virginianum Linnaeus var. *virginianum*—John's-cabbage (Figure 29). 2*n* = 18. Rich, deciduous, often wet, woodlands.

PHACELIA BRACHYLOBA (Bentham) A. Gray—(Figure 29). 2*n* = ? Wool waste, waste places. From California, Baja Mexico.

PHACELIA DISTANS Bentham—(Figure 29). 2*n* = 24. Wool waste. From southwestern United States, Baja Mexico.

PHACELIA EGENA (Brand) Greene *ex* J.T. Howell—(Figure 29). 2*n* = 22. Wool waste. From California. [*P. MAGELLANICA* (Lamarck) Coville]

PHACELIA MINOR (Harvey) Thellung *ex* F. Zimmerman—(Figure 29). 2*n* = ? Wool waste. From California, Baja Mexico.

LAMIACEAE

AGASTACHE FOENICULUM (Pursh) Kuntze—Blue Giant Hyssop (Figure 30). 2*n* = 18. Waste places, woodland margins, fields. From farther west.

Agastache nepetoides (Linnaeus) Kuntze—Yellow Giant Hyssop (Figure 30). 2*n* = 18. Roadsides, thickets, open woodlands.

Agastache scrophulariifolia (Willdenow) Kuntze—Purple Giant Hyssop (Figure 30). 2*n* = 18. Thickets, rich, open woodlands, streambanks, roadsides. [*A. scrophulariifolia* var. *mollis* (Fernald) A. Heller]

AJUGA GENEVENSIS Linnaeus—(Figure 30). 2*n* = 32. Fields, waste places, roadsides, dry ledge outcrops, usually in calcareous soil. From Eurasia.

AJUGA REPTANS Linnaeus—(Figure 30). 2*n* = 32. Moist shade, roadsides, fields, wet meadows, woodland margins. From Eurasia, northwestern Africa.

BALLOTA NIGRA Linnaeus var. *NIGRA*—Black Horehound (Figure 30). 2*n* = 20, (22). Waste places, roadsides, calcareous hillsides. From Eurasia, northwestern Africa.

Blephilia ciliata (Linnaeus) Bentham—(Figure 30). 2*n* = ? Fields, river meadows, woodlands, roadsides, railroads.

Blephilia hirsuta (Pursh) Bentham var. *hirsuta*—(Figure 30). 2*n* = ? Moist woodlands.

Blephilia hirsuta (Pursh) Bentham var. *glabrata* Fernald—(Figure 30). 2*n* = ? Dry fields.

CLINOPODIUM ACINOS (Linnaeus) Kuntze—Mother-of-Thyme (Figure 31). 2*n* = 18. Fields, roadsides, railroads, waste places, often in rocky sites. From Eurasia. [*Satureja acinos* (Linnaeus) Scheele]

Clinopodium vulgare Linnaeus—Wild Basil (Figure 31). 2*n* = 20. Thickets, woodlands, clearings, fields, roadsides, ledges. [*Satureja vulgaris* (Linnaeus) Fritsch var. *neogaea* Fernald]

Collinsonia canadensis Linnaeus—Richweed (Figure 31). 2*n* = 50. Rich, moist woodlands.

DRACOCEPHALUM MOLDAVICA Linnaeus—(Figure 31). 2*n* = 10. Wool waste. From Asia.

DRACOCEPHALUM PARVIFLORUM Nuttall—American Dragonhead (Figure 31). 2*n* = 14. Waste places, fields. From farther west.

ELSHOLTZIA CILIATA (Thunberg) Hylander—(Figure 31). 2*n* = 16, 18, 32. Waste places, roadsides, railroads, fields. From Asia.

GALEOPSIS BIFIDA Boenninghausen—(Figure 31). 2*n* = 32. Roadsides, waste places, fields. From Eurasia. [*G. TETRAHIT* Linnaeus var. *BIFIDA* (Boenninghausen) Lejeune & Courtois]

GALEOPSIS LADANUM Linnaeus var. *LADANUM*—(Figure 31). 2*n* = 16. Waste places, sea beaches, meadows. From Eurasia. [*G. LADANUM* var. *LATIFOLIA* (Hoffman) Wallroth]

GALEOPSIS TETRAHIT Linnaeus—(Figure 31). 2*n* = 32. Woodlands, fields, roadsides, waste places. From Eurasia.

GLECHOMA HEDERACEA Linnaeus—Gill-over-the-ground (Figure 32). 2*n* = 18, 36. Roadsides, moist woodlands, damp, shaded places, waste places. From Eurasia. [*G. HEDERACEA* var. *MICRANTHA* Moricand]

HEDEOMA HISPIDA Pursh—(Figure 32). 2*n* = 18, 38. Dry fields, calcareous ledges, roadsides. From farther west and south.

Hedeoma pulegioides (Linnaeus) Persoon—American False Pennyroyal (Figure 32). 2*n* = 38. Dry fields, ledges, roadsides.

HYSSOPUS OFFICINALIS Linnaeus—Hyssop (Figure 32). 2*n* = 12. Roadsides, dry fields, waste places. From Eurasia, northwestern Africa.

LAMIUM AMPLEXICAULE Linnaeus—Henbit (Figure 32). 2*n* = 18. Waste places, roadsides, fields. From Eurasia, northern Africa.

LAMIUM GALEOBDOLON (Linnaeus) Linnaeus—(Figure 32). 2*n* = 18. Roadside thickets, *Quercus* woodlands. From Eurasia.

LAMIUM MACULATUM Linnaeus—(Figure 32). 2*n* = 18. Roadsides, waste places. From Eurasia.

LAMIUM PURPUREUM Linnaeus var. *PURPUREUM*—Purple Dead-nettle (Figure 32). $2n = 18$. Waste places, roadsides, fields. From Eurasia, northwestern Africa.

LAMIUM PURPUREUM Linnaeus var. *INCISUM* (Willdenow) Persoon—(Figure 32). $2n = ?$ Waste places, roadsides. From Eurasia, northwestern Africa. [*L. HYBRIDUM* misapplied]

LEONURUS CARDIACA Linnaeus subsp. *CARDIACA*—Common Motherwort (Figure 33). $2n = 18$. Waste places, roadsides, woodland margins. From Eurasia.

Lycopus americanus Muhlenberg *ex* W.P.C. Barton—(Figure 33). $2n = 22$. Swampy woodlands, thickets, shores.

Lycopus amplectens Rafinesque—(Figure 33). $2n = 22$. Pond shores, bogs, swamps, in damp, sandy or peaty, soil. [*L. amplectens* var. *pubens* (Britton *ex* Small) Fernald]

LYCOPUS EUROPAEUS Linnaeus—(Figure 33). $2n = 22$. Waste places, roadsides. From Eurasia. [*L. EUROPAEUS* var. *MOLLIS* (J. Kerner) Briquet]

Lycopus rubellus Moench—(Figure 33). $2n = 22$. Wet fields, swamps, thickets, shores.

Lycopus uniflorus Michaux var. *uniflorus*—Northern Bugleweed (Figure 33). $2n = 22$. Shady, moist places, swamps, shores.

Lycopus virginicus Linnaeus—(Figure 33). $2n = 22$. Swampy woodlands, shores, wetland margins.

— *Lycopus* hybrid —

Lycopus × *sherardii* E.S. Steele (*pro species*)—(Figure 33). [*L. uniflorus* Michaux × *L. virginicus* Linnaeus]

MARRUBIUM VULGARE Linnaeus—Common Horehound (Figure 33). $2n = 34$. Waste places, roadsides. From Eurasia, northwestern Africa.

MELISSA OFFICINALIS Linnaeus—Common Balm (Figure 34). $2n = 32, 64$. Waste places, roadsides. From Eurasia, northwestern Africa.

MENTHA AQUATICA Linnaeus var. *CITRATA* (Ehrhart) Fresenius—Bergamot Mint (Figure 34). $2n = 96$. Waste places, roadsides. From Europe. [*M. CITRATA* Ehrhart]

MENTHA ARVENSIS Linnaeus subsp. *PARIETARIIFOLIA* (Becker) Briquet—Ginger Mint (Figure 34). $2n = 72$. Wet places, roadsides, fields, waste places. From Europe. [*M. GENTILIS* Linnaeus]

Mentha canadensis Linnaeus—American Corn Mint (Figure 34). $2n = 96$. Moist, open soils, shores, fields, roadsides. [*M. canadensis* var. *villosa* Bentham; *M. arvensis* var. *arvensis* misapplied; *M. arvensis* Linnaeus var. *canadensis* (Linnaeus) Kuntze; *M. arvensis* var. *villosa* (Bentham) S.R. Stewart]

MENTHA SPICATA Linnaeus var. *SPICATA*—Spearmint (Figure 34). 2*n* = 36, 48. Wet thickets, wet fields, shores, roadsides, waste places. From Europe. [*M. LONGIFOLIA* var. *LONGIFOLIA* misapplied; *M. LONGIFOLIA* var. *MOLLISSIMA* misapplied]

MENTHA SUAVEOLENS Ehrhart subsp. *SUAVEOLENS*—Apple Mint (Figure 34). 2*n* = 24. Swales, waste places. From Europe.

— *Mentha* hybrids —

MENTHA × *GRACILIS* Sole (*pro species*)—(Figure 34). [*M. ARVENSIS* Linnaeus × *M. SPICATA* Linnaeus; *M. CARDIACA* J. Gerarde *ex* Baker]

MENTHA × *PIPERITA* Linnaeus (*pro species*)—(Figure 34). [*M. AQUATICA* Linnaeus × *M. SPICATA* Linnaeus; *M. CRISPA* Linnaeus]

MENTHA × *ROTUNDIFOLIA* (Linnaeus) Hudson (*pro species*)—(Figure 34). [*M. LONGIFOLIA* (Linnaeus) Linnaeus × *M. SUAVEOLENS* Ehrhart]

MENTHA × *SMITHIANA* R.A. Graham—(Figure 35). [*M. AQUATICA* Linnaeus × *M. ARVENSIS* Linnaeus × *M. SPICATA* Linnaeus]

MENTHA × *VERTICILLATA* Linnaeus (*pro species*)—(Figure 35). [*M. AQUATICA* Linnaeus × *M. ARVENSIS* Linnaeus]

MENTHA × *VILLOSA* Hudson (*pro species*)—(Figure 35). [*M. SPICATA* Linnaeus × *M. SUAVEOLENS* Ehrhart; *M. ALOPECUROIDES* Hull]

MONARDA CLINOPODIA Linnaeus—Basil Bee-balm (Figure 35). 2*n* = ? Roadsides, low woodlands. From farther south and west.

MONARDA DIDYMA Linnaeus—Oswego-tea (Figure 35). 2*n* = 36. Roadsides, waste places, woodland margins, thickets, fields, clearings. From farther south and west.

Monarda fistulosa Linnaeus var. *fistulosa*—Wild Bergamot (Figure 35). 2*n* = 18, 36. Roadsides, woodlands, clearings, thickets, meadows, fields, railroads, streambanks, waste places.

Monarda fistulosa Linnaeus var. *mollis* (Linnaeus) Bentham—(Figure 35). 2*n* = ? Fields, roadsides, open woodlands, fencerows, waste places.

MONARDA MEDIA Willdenow—Purple Bergamot (Figure 35). 2*n* = 36. Roadsides, thickets, fencerows, woodland margins. From farther west and south. [*M. FISTULOSA* var. *RUBRA* misapplied]

Monarda punctata Linnaeus var. *villicaulis* (Pennell) E.J. Palmer & Steyermark—(Figure 35). 2*n* = ? Sandy fields and roadsides, dry, sandy soil.

NEPETA CATARIA Linnaeus—Catnip (Figure 36). 2*n* = 34, 36. Fields, waste places, roadsides, deciduous woodlands. From Eurasia.

OCIMUM BASILICUM Linnaeus—Sweet Basil (Figure 36). $2n$ = (30), 48, 52, 72. Waste places. Possibly from Africa.

ORIGANUM VULGARE Linnaeus subsp. *VULGARE*—Wild Marjoram (Figure 36). $2n$ = 30, 32. Waste places, roadsides, railroads, fields, woodlands, brooksides, meadows. From Eurasia, northwestern Africa.

PERILLA FRUTESCENS (Linnaeus) Britton var. *FRUTESCENS*—(Figure 36). $2n$ = 40. Waste places, roadsides, fields. From southern and eastern Asia. [*P. OCYMOIDES* Linnaeus]

PERILLA FRUTESCENS (Linnaeus) Britton var. *CRISPA* (Bentham) W. Deane—(Figure 36). $2n$ = ? Waste places, roadsides. Known only from cultivation.

PEROVSKIA ATRIPLICIFOLIA Bentham—(Figure 36). $2n$ = 20. Roadsides. From Asia.

Physostegia virginiana (Linnaeus) Bentham subsp. *virginiana*—Obedient-plant (Figure 36). $2n$ = 38. Roadsides, fields, streambanks, damp thickets, shores. [*P. virginiana* var. *granulosa* (Fassett) Fernald; *P. virginiana* var. *speciosa* (Sweet) A. Gray]

PRUNELLA VULGARIS Linnaeus subsp. *VULGARIS*—Heal-all (Figure 36). $2n$ = 28. Fields, roadsides, waste places. From Eurasia, northwestern Africa.

Prunella vulgaris Linnaeus subsp. *lanceolata* (W.P.C. Barton) Piper & Beattie—(Figure 36). $2n$ = 28. Open, moist woodlands, meadows, streambanks, fields, thickets, roadsides.

Pycnanthemum incanum (Linnaeus) Michaux var. *incanum*—(Figure 37). $2n$ = 76. Dry woodlands, thickets.

Pycnanthemum muticum (Michaux) Persoon—(Figure 37). $2n$ = ca. 108. Dry woodlands, thickets, clearings.

PYCNANTHEMUM PILOSUM Nuttall—(Figure 37). $2n$ = ? Woodland margins, thickets, dry knolls, sandy fields. From farther west.

Pycnanthemum tenuifolium Schrader—(Figure 37). $2n$ = 40. Dry fields, thickets, clearings, roadsides.

Pycnanthemum torreyi Bentham—(Figure 37). $2n$ = 78-80. Dry, rocky woodlands, dry, gravelly banks, meadows.

Pycnanthemum verticillatum (Michaux) Persoon—(Figure 37). $2n$ = 76-78. Woodlands, fields, meadows, thickets, clearings, usually in moist soil.

Pycnanthemum virginianum (Linnaeus) B.L. Robinson & Fernald—(Figure 37). $2n$ = 80. Fields, shores, meadows, woodlands, thickets, roadsides, usually in moist soil.

— *Pycnanthemum* hybrid —

Pycnanthemum × *clinopodioides* Torrey & A. Gray (*pro species*)—(Figure 37). [*P. incanum* (Linnaeus) Michaux × *P. verticillatum* (Michaux) Persoon]

SALVIA AZUREA Michaux *ex* Vahl var. *GRANDIFLORA* Bentham—Blue Sage (Figure 37). 2*n* = ? Waste places, sidewalks. From farther west. [*S. PITCHERI* Torrey *ex* Bentham]

SALVIA FARINACEA Bentham—Mealy-cup Sage (Figure 38). 2*n* = 18, 20. Roadsides. From south central United States.

Salvia lyrata Linnaeus—Cancerweed (Figure 38). 2*n* = 36. Meadows.

SALVIA OFFICINALIS Linnaeus—Garden Sage (Figure 38). 2*n* = 14. Roadsides, fields, fencerows, river thickets. From southeastern Europe.

SALVIA PRATENSIS Linnaeus—Meadow Sage (Figure 38). 2*n* = 16, 18, (32). Waste places, fields, grassy hillsides, roadsides. From Europe.

SALVIA SCLAREA Linnaeus—Clary Sage (Figure 38). 2*n* = 22. Waste places, fencerows. From Eurasia.

SALVIA SPLENDENS Sellow *ex* Nees—Scarlet Sage (Figure 38). 2*n* = 44. Waste places. From Brazil.

SALVIA SYLVESTRIS Linnaeus—(Figure 38). 2*n* = 14. Roadsides, fields. From Eurasia. [*S. NEMOROSA* Linnaeus]

SALVIA TILIIFOLIA Vahl—(Figure 38). 2*n* = 22. Waste places. From Mexico, Central and South America.

SALVIA VERTICILLATA Linnaeus—Lilac Sage (Figure 38). 2*n* = 16. Fields, meadows, waste places, roadsides. From Eurasia.

SATUREJA HORTENSIS Linnaeus—Summer Savory (Figure 39). 2*n* = 48. Waste places, fields, railroads, roadsides, gravelly banks. From Eurasia.

Scutellaria galericulata Linnaeus—Marsh Skullcap (Figure 39). 2*n* = 30, 32. Swamps, shores, meadows, marshes. [*S. epilobiifolia* A. Hamilton]

Scutellaria integrifolia Linnaeus—(Figure 39). 2*n* = 32. Fields, meadows.

Scutellaria lateriflora Linnaeus var. *lateriflora*—Mad-dog Skullcap (Figure 39). 2*n* = 80, 88. Wet woodlands, shores, meadows, alluvial thickets, marshes.

Scutellaria parvula Michaux var. *parvula*—(Figure 39). 2*n* = 20. Rocky outcrops of shores and fields.

Scutellaria parvula Michaux var. *missouriensis* (Torrey) Goodman & C.A. Lawson—(Figure 39). 2*n* = ? Rocky outcrops of shores, fields, ridges, hills, and open woodlands. [*S. parvula* var. *leonardi* (Epling) Fernald]

— *Scutellaria* hybrid —

Scutellaria × *churchilliana* Fernald (*pro species*)—(Figure 39). [*S. galericulata* Linnaeus × *S. lateriflora* Linnaeus]

SIDERITIS MONTANA Linnaeus—(Figure 39). 2*n* = 16, 32. Waste places, dry, open ground. From Eurasia, northwestern Africa.

STACHYS ANNUA (Linnaeus) Linnaeus—(Figure 39). 2*n* = 34. Waste places. From Eurasia.

STACHYS ARVENSIS (Linnaeus) Linnaeus—Staggerweed (Figure 40). 2*n* = 10. Waste places. From Eurasia, northwestern Africa.

STACHYS ASPERA Michaux—(Figure 40). 2*n* = ca. 60, 68. Roadsides. From farther south and west. [*S. HYSSOPIFOLIA* Michaux var. *AMBIGUA* A. Gray]

STACHYS BYZANTINA K. Koch—Lamb's-ears (Figure 40). 2*n* = 30. Waste places, fields, swamp margins. From Caucasus region.

STACHYS GERMANICA Linnaeus—(Figure 40). 2*n* = 30. Waste places. From Eurasia, northwestern Africa.

Stachys hispida Pursh—(Figure 40). 2*n* = 68. Meadows, swamps, low woodlands, shores, damp thickets. [*S. tenuifolia* Willdenow var. *hispida* (Pursh) Fernald; *S. tenuifolia* Willdenow var. *platyphylla* misapplied]

Stachys hyssopifolia Michaux—(Figure 40). 2*n* = 34. Sandy pond shores.

STACHYS PALUSTRIS Linnaeus—Woundwort (Figure 40). 2*n* = 64, 96, 102. Shores, damp thickets, wet roadsides, low meadows, waste places. From Eurasia. [*S. PALUSTRIS* var. *ELLIPTICA* Clos; *S. PALUSTRIS* var. *SEGETUM* (Mutel) Grognier]

Stachys pilosa Nuttall var. *pilosa*—(Figure 40). 2*n* = 64. Shores, meadows, fields, low grounds. [*S. palustris* Linnaeus var. *homotricha* Fernald; *S. palustris* var. *nipigonensis* Jennings; *S. palustris* var. *pilosa* (Nuttall) Fernald]

STACHYS PILOSA Nuttall var. *ARENICOLA* (Britton) G.A. Mulligan & D.B. Munro—(Figure 40). 2*n* = 68. Wet grounds. From farther west.

TEUCRIUM BOTRYS Linnaeus—Cut-leaf Germander (Figure 41). 2*n* = 32. Dry or rocky fields, often calcareous. From Europe.

Teucrium canadense Linnaeus var. *canadense*—American Germander (Figure 41). 2*n* = 32. Salt marsh margins, wet woodlands, shores, wet thickets. [*T. canadense* var. *virginicum* (Linnaeus) Eaton]

Teucrium canadense Linnaeus var. *occidentale* (A. Gray) E.M. McClintock & Epling—(Figure 41). 2*n* = ? Alluvial soil, shores. [*T. occidentale* A. Gray var. *occidentale*; *T. occidentale* A. Gray var. *boreale* (E.P. Bicknell) Fernald]

TEUCRIUM SCORODONIA Linnaeus—Wood Germander (Figure 41). 2*n* = 32, (34). Open woodlands. From Europe, northwestern Africa.

THYMUS PULEGIOIDES Linnaeus—Lemon Thyme (Figure 41). $2n = 28$. Dry fields, roadsides, waste places. From Europe. [*T. SERPYLLUM* misapplied]

Trichostema brachiatum Linnaeus—False Pennyroyal (Figure 41). $2n = 14$. Woodland borders, hillsides, ledges, in dry, often calcareous, soil. [*Isanthus brachiatus* (Linnaeus) Britton, Sterns & Poggenburg]

Trichostema dichotomum Linnaeus—Bluecurls (Figure 41). $2n = 38$. Dry, open, sandy soil, waste places, roadsides, fields.

Trichostema setaceum Houttuyn—(Figure 41). $2n = 38$. Dry sands.

LINACEAE

LINUM CATHARTICUM Linnaeus—Fairy Flax (Figure 41). $2n = 16$. Fields, roadsides, in calcareous or sandy soil. From Eurasia, northwestern Africa.

Linum intercursum E.P. Bicknell—(Figure 42). $2n = 36$. Sandy beaches, open, sandy places.

Linum medium (Planchon) Britton var. *texanum* (Planchon) Fernald—(Figure 42). $2n = 36$. Dry fields, roadsides, in sterile, open soil.

LINUM PERENNE Linnaeus—Blue Flax (Figure 42). $2n = 18, 36$. Dry, sandy hills. From Eurasia.

Linum striatum Walter—(Figure 42). $2n = 36$. Damp thickets, bogs, meadows, shores. [*L. striatum* var. *multijugum* Fernald]

Linum sulcatum Riddell—(Figure 42). $2n = 30$. Roadsides, sandy fields, in dry, open soil.

LINUM USITATISSIMUM Linnaeus—Common Flax (Figure 42). $2n = 30$. Railroads, waste places, fields, roadsides. From Eurasia.

Linum virginianum Linnaeus—(Figure 42). $2n = 36$. Roadsides, dry, open woodlands, fields, thickets, clearings.

RADIOLA LINOIDES Roth—(Figure 42). $2n = 18$. Grassy turf bordering rocky beaches, pastures. From Eurasia, northern and central Africa. [*LINUM RADIOLA* Linnaeus; *MILLEGRANA RADIOLA* (Linnaeus) Druce]

LOASACEAE

MENTZELIA OLIGOSPERMA Nuttall *ex* Sims—(Figure 42). $2n = 22$. Wool waste. From farther west.

LYTHRACEAE

CUPHEA PROCUMBENS Ortega—(Figure 43). $2n = 18$. Pastures. From southern Mexico.

Cuphea viscosissima Jaquin—Blue Waxweed (Figure 43). $2n = 12$. Fields, roadsides. [*C. petiolata* Pohl *ex* Koehne]

Decodon verticillatus (Linnaeus) Elliott—Swamp Loosestrife (Figure 43). $2n = 32$. Pond and bog margins, shores, swamps, usually in shallow water. [*D. verticillatus* var. *laevigatus* Torrey & A. Gray]

LYTHRUM ALATUM Pursh var. *ALATUM*—Winged Loosestrife (Figure 43). $2n = 20$. Meadows, moist fields, streambanks, swamps, roadsides. From farther west and south.

Lythrum hyssopifolia Linnaeus—(Figure 43). $2n = 20$. Salt marsh margins, moist dune hollows.

LYTHRUM JUNCEUM Banks & Solander—(Figure 43). $2n = 10$. Sandy streambanks. From Mediterranean region.

LYTHRUM SALICARIA Linnaeus—Purple Loosestrife (Figure 43). $2n = 30, 60$. River meadows, swamps, marshes, shores, wet roadsides. From Eurasia, northwestern Africa. [*L. SALICARIA* var. *GRACILIOR* Turczaninow; *L. SALICARIA* var. *TOMENTOSUM* (Miller) de Candolle]

Rotala ramosior (Linnaeus) Koehne—Tooth-cup (Figure 43). $2n = 16$. Sandy or muddy shores of ponds and streams.

TRAPA NATANS Linnaeus—Water-chestnut (Figure 43). $2n = 44, 46, 48, 90$. Quiet streams, ponds. From Eurasia, Africa.

MELASTOMATACEAE

Rhexia mariana Linnaeus var. *mariana*—(Figure 44). $2n = 22, 44$. Pond shores.

Rhexia virginica Linnaeus—Common Meadow-beauty (Figure 44). $2n = 22, 44$. Peaty meadows, pond shores.

NYSSACEAE

Nyssa sylvatica Marshall—Black Tupelo (Figure 44). $2n = 44$. Swamps, shores, low, acidic woodlands.

OLEACEAE

CHIONANTHUS VIRGINICUS Linnaeus—Fringe-tree (Figure 44). $2n = 46$. Roadsides, woodland margins. From farther west and south.

FORSYTHIA SUSPENSA (Thunberg) Vahl—Weeping Forsythia (Figure 44). $2n = 24, 28$. Roadsides, woodland margins, railroads. From China. [*F. SUSPENSA* var. *FORTUNEI* (Lindley) Rehder]

FORSYTHIA VIRIDISSIMA Lindley—(Figure 44). $2n = 28$. Roadsides, damp thickets, streambanks. From China, Korea.

— *Forsythia* hybrid —

FORSYTHIA × *INTERMEDIA* Zabel (*pro species*)—(Figure 44). [parentage of current specimens uncertain, although parentage of the type specimen is *F. SUSPENSA* (Thunberg) Vahl × *F. VIRIDISSIMA* Lindley]

Fraxinus americana Linnaeus—White Ash (Figure 44). $2n = 46$. Rich woodlands, roadsides.

FRAXINUS EXCELSIOR Linnaeus—European Ash (Figure 44). $2n = 46$. Roadsides, wooded streambanks. From Eurasia.

Fraxinus nigra Marshall—Black Ash (Figure 45). $2n = 46$. Swamps, wet woodlands, shores.

Fraxinus pennsylvanica Marshall—Red Ash (Figure 45). $2n = 46$. Shores, swamps, alluvial woodlands. [*F. pennsylvanica* var. *austinii* Fernald; *F. pennsylvanica* var. *subintegerrima* (Vahl) Fernald]

LIGUSTRUM OBTUSIFOLIUM Siebold & Zuccarini subsp. *OBTUSIFOLIUM*—(Figure 45). $2n = 46$. Woodlands, woodland margins, thickets, roadsides, streambanks. From Japan, Korea.

LIGUSTRUM OBTUSIFOLIUM Siebold & Zuccarini subsp. *SUAVE* (Kitagawa) Kitagawa—Amur Privet (Figure 45). $2n = 46$. Thickets. From China. [*L. AMURENSE* Carrière]

LIGUSTRUM OVALIFOLIUM Hasskarl—California Privet (Figure 45). $2n = 46$. Roadsides, thickets, sandy, waste places. From Japan, Korea.

LIGUSTRUM SINENSE Loureiro—Chinese Privet (Figure 45). $2n = 46$. Railroads. From eastern Asia.

LIGUSTRUM VULGARE Linnaeus—Common Privet (Figure 45). $2n = 46$. Roadsides, thickets, open woodlands. From Eurasia, northwestern Africa.

SYRINGA RETICULATA (Blume) H. Hara subsp. *RETICULATA*—Japanese Tree Lilac (Figure 45). $2n = ?$ Roadsides, woodland margins. From Japan.

SYRINGA VILLOSA Vahl—(Figure 45). $2n = 46$. Wooded bank. From China.

SYRINGA VULGARIS Linnaeus—Common Lilac (Figure 46). $2n = 38, 44, 46$. Roadsides, woodland margins. From southeastern Europe.

— *Syringa* hybrids —

SYRINGA × *CHINENSIS* Willdenow (*pro species*)—(Figure 46). [*S.* × *PERSICA* Linnaeus × *S. VULGARIS* Linnaeus]

SYRINGA × *PERSICA* Linnaeus (*pro species*)—(Figure 46). [*S. PROTOLACINIATA* P.S. Green & M.C. Chang × *S. VULGARIS* Linnaeus]

ONAGRACEAE

CAMISSONIA CAMPESTRIS (Greene) P.H. Raven subsp. *CAMPESTRIS*—Mojave Suncup (Figure 46). $2n = ?$ Wool waste. From southwestern United States.

CAMISSONIOPSIS BISTORTA (Nuttall *ex* Torrey & A. Gray) W.L. Wagner & Hoch—California Suncup (Figure 46). $2n = ?$ Wool waste. From southern California.

Chamaenerion angustifolium (Linnaeus) Scopoli subsp. *circumvagum* (Mosquin) Moldenke—Fireweed (Figure 46). $2n = 72$ Burned woodlands, recent clearings, thickets, roadsides, fields. [*Chamerion angustifolium* (Linnaeus) Holub subsp. *circumvagum* (Mosquin) Hoch; *Epilobium angustifolium* Linnaeus var. *angustifolium* misapplied; *E. angustifolium* var. *canescens* Alph. Wood]

Circaea alpina Linnaeus subsp. *alpina*—Smaller Enchanter's Nightshade (Figure 46). $2n = 22$. Swampy or springy woodlands, streambanks.

Circaea canadensis (Linnaeus) Hill—Common Enchanter's Nightshade (Figure 46). $2n = 22$. Rich, moist woodlands. [*C. lutetiana* Linnaeus var. *canadensis* Linnaeus; *C. quadrisulcata* (Maximowicz) Franchet & Savatier var. *canadensis* (Linnaeus) H. Hara]

— *Circaea* hybrid —

Circaea × *sterilis* Boufford—(Figure 46). [*C. alpina* Linnaeus × *C. canadensis* (Linnaeus) Hill]

CLARKIA PULCHELLA Pursh—(Figure 47). $2n = ?$ Fields, meadows, waste places. From northwestern United States.

CLARKIA RHOMBOIDEA Douglas—(Figure 47). $2n = 24$. Wool waste. From western United States.

Epilobium anagallidifolium Lamarck—(Figure 47). $2n = 36$. Alpine areas. [*E. alpinum* Linnaeus, rejected name, in part]

Epilobium ciliatum Rafinesque subsp. *ciliatum*—(Figure 47). $2n = 36$. Wet, open woodlands, damp thickets and fields, shores, marshes. [*E. glandulosum* Lehmann var. *adenocaulon* (Haussknecht) Fernald]

Epilobium ciliatum Rafinesque subsp. *glandulosum* (Lehmann) Hoch & P.H. Raven—(Figure 47). $2n = ?$ Damp thickets. [*E. glandulosum* Lehmann var. *cardiophyllum* Fernald; *E. glandulosum* var. *occidentale* (Trelease) Fernald]

Epilobium coloratum Biehler—Eastern Willow-herb (Figure 47). $2n = 36$. Swamps, boggy thickets, springy slopes, shores, marshes.

EPILOBIUM HIRSUTUM Linnaeus—(Figure 47). $2n = 36$. Waste places, roadside thickets, meadows. From Eurasia, Africa.

Epilobium hornemannii Reichenbach subsp. *hornemannii*—(Figure 47). $2n = 36$. Margins of brooks, damp rocks, at high altitudes, often in wet moss.

Epilobium lactiflorum Haussknecht—(Figure 47). 2*n* = 36. Alpine areas. [*E. alpinum* Linnaeus, rejected name, in part]

Epilobium leptophyllum Rafinesque—(Figure 48). 2*n* = 36. Bogs, swamps, meadows, marshes.

Epilobium palustre Linnaeus—(Figure 48). 2*n* = 36. Bogs, swamps, meadows, swales. [*E. palustre* var. *grammadophyllum* Haussknecht; *E. palustre* var. *labradoricum* Haussknecht; *E. palustre* var. *oliganthum* (Michaux) Fernald]

Epilobium strictum Muhlenberg *ex* Sprengel—(Figure 48). 2*n* = 36. Bogs, swamps, meadows, mossy thickets, marshes, shores.

Ludwigia alternifolia Linnaeus—Seedbox (Figure 48). 2*n* = 16. Pond and stream shores, swamps, marshes.

Ludwigia palustris (Linnaeus) Elliott—Common Water-purslane (Figure 48). 2*n* = 16. Pond and stream shores, swamps. [*L. palustris* var. *americana* (de Candolle) Fernald & Griscom]

Ludwigia polycarpa Short & R. Peter—(Figure 48). 2*n* = 32. Pond and stream shores.

Ludwigia sphaerocarpa Elliott—(Figure 48). 2*n* = 32. Pond and stream shores, marshes. [*L. sphaerocarpa* var. *macrocarpa* Fernald & Griscom]

— *Ludwigia* hybrid —

Ludwigia × *lacustris* Eames (*pro species*)—(Figure 48). [*L. BREVIPES* (Long) Eames × *L. palustris* (Linnaeus) Elliott]

OENOTHERA AFFINIS Cambessèdes—(Figure 48). 2*n* = ? Waste places. From South America.

Oenothera biennis Linnaeus—Common Evening-Primrose (Figure 49). 2*n* = 14. Roadsides, fields, waste places, river thickets. [*O. biennis* var. *pycnocarpa* (G.F. Atkinson & Bartlett) Wiegand]

OENOTHERA CURTIFLORA W.L. Wagner & Hoch—(Figure 49). 2*n* = 14. Waste places. From farther west. [*GAURA PARVIFLORA* Douglas *ex* Lehmann]

Oenothera fruticosa Linnaeus subsp. *fruticosa*—Southern Sundrops (Figure 49). 2*n* = 56. Salt marsh margins, meadows, swamps, fields. [*O. fruticosa* var. *eamesii* (B.L. Robinson) S.F. Blake; *O. fruticosa* var. *humifusa* Allen; *O. fruticosa* var. *linearis* (Michaux) S. Watson; *O. tetragona* Roth var. *longistipata* (Pennell) Munz]

Oenothera fruticosa Linnaeus subsp. *tetragona* (Roth) W.L. Wagner—(Figure 49). 2*n* = 28. Gravelly, sandy eskers, dry fields and banks, woodland margins, waste places. [*O. fruticosa* Linnaeus subsp. *glauca* (Michaux) Straley; *O. tetragona* Roth var. *tetragona*]

OENOTHERA GAURA W.L. Wagner & Hoch—(Figure 49). 2*n* = 14. Roadsides, waste places, dry thickets. From farther south and west. [*GAURA BIENNIS* Linnaeus]

OENOTHERA GLAZIOVIANA Micheli—(Figure 49). 2*n* = 14. Roadsides, waste places, fields. From farther south and west. [*O. ERYTHROSEPALA* Borbás]

OENOTHERA GRANDIFLORA L'Héritier—(Figure 49). $2n = 14$. Roadsides, waste places. From farther south. [*O. BIENNIS* Linnaeus var. *GRANDIFLORA* (L'Héritier *ex* Aiton) Torrey & A. Gray]

OENOTHERA GRANDIS (Britton) Smyth—(Figure 49). $2n = 14$. Fields. From farther west.

OENOTHERA LACINIATA Hill—(Figure 49). $2n = 14$. Waste places, roadsides, fields, usually in dry, sandy, open soil. From farther south and west.

Oenothera mutans G.F. Atkinson & Bartlett—(Figure 50). $2n = 14$. River thickets. [*O. biennis* Linnaeus var. *mutans* (G.F. Atkinson & Bartlett) Wiegand]

Oenothera oakesiana (A. Gray) J.W. Robbins *ex* S. Watson & J.M. Coulter—(Figure 50). $2n = 14$. Open, sandy areas of beaches, dunes, roadsides and fields. [*O. cruciata* Nuttall *ex* G. Don var. *stenopetala* (E.P. Bicknell) Fernald; *O. parviflora* Linnaeus var. *angustissima* (R.R. Gates) Wiegand; *O. parviflora* Linnaeus var. *oakesiana* (A. Gray) Fernald)]

Oenothera parviflora Linnaeus—(Figure 50). $2n = 14$. Streambanks, thickets, roadsides, railroads, fields, dry sand or gravel. [*O. biennis* Linnaeus var. *cruciata* (Nuttall *ex* G. Don) Torrey & A. Gray; *O. cruciata* Nuttall *ex* G. Don var. *cruciata*]

Oenothera perennis Linnaeus—Little Sundrops (Figure 50). $2n = 14$. Dry fields, clearings, roadsides, waste places, meadows.

OENOTHERA PILOSELLA Rafinesque—(Figure 50). $2n = 56$. Dry woodlands, fields, roadsides, rocky shores, waste places. From farther west and south.

OENOTHERA SERRULATA Nuttall—(Figure 50). $2n = 14$. Railroads. From farther west. [*CALYLOPHUS SERRULATUS* (Nuttall) P.H. Raven]

OENOTHERA SPECIOSA Nuttall—White Evening-Primrose (Figure 50). $2n = 14$. Waste places, roadsides. From farther west and south.

OENOTHERA VILLOSA Thunberg subsp. *VILLOSA*—(Figure 50). $2n = 14$. Fields, roadsides, waste places, beaches. From farther west. [*O. DEPRESSA* Greene]

OXALIDACEAE

OXALIS CORNICULATA Linnaeus—Creeping Wood-Sorrel (Figure 50). $2n = 24, 44$. Waste places, roadsides, fields. From unknown origin.

Oxalis dillenii Jacquin—(Figure 51). $2n = 18, 20, 22, 20\text{-}24$. Dry fields, sandy thickets, woodland margins, roadsides, waste areas. [*O. filipes* Small; *O. florida* Salisbury; *O. stricta* misapplied]

Oxalis montana Rafinesque—Mountain Wood-Sorrel (Figure 51). $2n = 22$. Rich, damp woodlands. [*O. acetosella* misapplied]

Oxalis stricta Linnaeus—(Figure 51). 2*n* = 18, 24. Waste places, roadsides, fields. [*O. europaea* Jordan var. *europaea*; *O. europaea* var. *bushii* (Small) Wiegand]

Oxalis violacea Linnaeus—Violet Wood-Sorrel (Figure 51). 2*n* = 28. Rich, moist woodlands, rocky slopes. [*O. violacea* var. *trichophora* Fassett]

— *Oxalis* hybrid —

Oxalis dillenii Jacquin × *O. stricta* Linnaeus—(Figure 51).

POLEMONIACEAE

COLLOMIA LINEARIS Nuttall—(Figure 51). 2*n* = 16. Railroads, meadows, waste places, wool waste. From farther west.

GILIA ACHILLEIFOLIA Bentham subsp. *MULTICAULIS* V.D. Grant & A.D. Grant—(Figure 51). 2*n* = 18. Waste places. From California.

GILIA INTERIOR (H. Mason & A.D. Grant) A.D. Grant—(Figure 51). 2*n* = 18. Wool waste. From California.

GILIA TRICOLOR Bentham subsp. *DIFFUSA* (Congdon) H. Mason & A.D. Grant—(Figure 51). 2*n* = 18 Waste places. From California.

IPOMOPSIS RUBRA (Linnaeus) Wherry—Standing-cypress (Figure 52). 2*n* = 14. Sandy soil. From farther south and west. [*GILIA RUBRA* (Linnaeus) A. Heller]

NAVARRETIA LEUCOCEPHALA Bentham subsp. *MINIMA* (Nuttall) A.G. Day—(Figure 52). 2*n* = 18. Wool waste. From western United States.

PHLOX BIFIDA L.C. Beck subsp. *BIFIDA*—Sand Phlox (Figure 52). 2*n* = ? Shaded, sandy soil near cemetery. From farther west.

Phlox divaricata Linnaeus subsp. *divaricata*—Wild Blue Phlox (Figure 52). 2*n* = 14. Damp, rocky, rich woodlands, waste places.

Phlox maculata Linnaeus subsp. *maculata*—Wild Sweet William (Figure 52). 2*n* = 14. Meadows, alluvial woodlands, streambanks, swamps, roadsides.

PHLOX PANICULATA Linnaeus—Fall Phlox (Figure 52). 2*n* = 14. Roadsides, woodland margins, fields, thickets. From farther west and south.

Phlox pilosa Linnaeus subsp. *pilosa*—(Figure 52). 2*n* = 14. Moist, grassy banks, dry knolls.

PHLOX STOLONIFERA Sims—Creeping Phlox (Figure 52). 2*n* = 24. Cemeteries, roadsides. From farther south.

PHLOX SUBULATA Linnaeus subsp. *SUBULATA*—Moss Phlox (Figure 52). 2*n* = 14. Cemeteries, sandy fields and roadsides, waste places. From farther west and south.

— *Phlox* hybrid —

PHLOX × *PROCUMBENS* Lehmann (*pro species*)—(Figure 53). [*P. STOLONIFERA* Sims × *O. SUBULATA* Linnaeus]

POLEMONIUM CAERULEUM Linnaeus subsp. *CAERULEUM*—Charity (Figure 53). 2*n* = 18. Cemeteries, roadsides, waste places. From Eurasia.

POLEMONIUM REPTANS Linnaeus var. *REPTANS*—(Figure 53). 2*n* = 18. Fields, roadsides, marshes, swamps. From farther west and south.

Polemonium vanbruntiae Britton—(Figure 53). 2*n* = 18. Bogs, swamps.

POLYGALACEAE

Polygala ambigua Nuttall—(Figure 53). 2*n* = ? Open woodlands, fields, plains, roadsides, often in sandy soil. [*P. verticillata* Linnaeus var. *ambigua* (Nuttall) Alph. Wood]

Polygala cruciata Linnaeus var. *aquilonia* Fernald & B.G. Schubert—(Figure 53). 2*n* = ? Meadows, pond shores. marshes, usually in peaty or sandy soil.

Polygala nuttallii Torrey & A. Gray—(Figure 53). 2*n* = 46. Dry, sandy fields, open woodlands, railroads, and other dry, sandy open soil.

Polygala paucifolia Willdenow—Fringed Polygala (Figure 53). 2*n* = 34. Woodlands, woodland margins, in rich, light soil. [*Polygaloides paucifolia* (Willdenow) J.R. Abbott]

Polygala polygama Walter—(Figure 53). 2*n* = 56. Fields, woodlands, openings, in dry, sandy soil. [*P. polygama* var. *obtusata* Chodat]

Polygala sanguinea Linnaeus—(Figure 54). 2*n* = ? Fields, meadows, other, moist, open, acid soils.

Polygala senega Linnaeus—Seneca-Snakeroot (Figure 54). 2*n* = 34. River terraces, dry woodlands, dry rocky or gravelly areas, usually in calcareous soil.

Polygala verticillata Linnaeus var. *verticillata*—(Figure 54). 2*n* = 34. Fields, open, rocky areas, roadsides, railroads, in sterile, open soil. [*P. verticillata* var. *isocycla* Fernald]

RHAMNACEAE

Ceanothus americanus Linnaeus—New Jersey Tea (Figure 54). 2*n* = 24. Thickets, open woodlands, rocky or gravelly banks, roadsides, in dry, open soil. [*C. americanus* var. *intermedius* (Pursh) Torrey & A. Gray]

Ceanothus herbaceus Rafinesque—Prairie Redroot (Figure 54). 2*n* = 24. Lake shores, fields, in dry, open, sandy soil. [*C. ovatus* Desfontaines]

FRANGULA ALNUS Miller—Glossy Buckthorn (Figure 54). $2n = 20$. Woodlands, thickets, roadsides, fields, ledge crevices. From Eurasia, northwestern Africa. [*RHAMNUS FRANGULA* Linnaeus]

Rhamnus alnifolia L'Héritier—American Alder Buckthorn (Figure 54). $2n = 24$. Bogs, swamps, damp thickets, often with *Thuja*.

RHAMNUS CATHARTICA Linnaeus—Common Buckthorn (Figure 54). $2n = 24$. Hedgerows, thickets, roadsides, fields, open woodlands. From Eurasia, northwestern Africa.

RHAMNUS DAVURICA Pallas subsp. *DAVURICA*—(Figure 54). $2n = 24$. Roadsides, woodlands. From eastern Asia. [*R. CITRIFOLIA* misapplied]

RUTACEAE

DICTAMNUS ALBUS Linnaeus—Gas Plant (Figure 55). $2n = 36$. Ledges, woodlands. From Eurasia.

PHELLODENDRON AMURENSE Ruprecht—Amur Corktree (Figure 55). $2n = 28$, ca. 66, 78, ca. 80. Woodlands, roadsides, swamps, pond shores. From eastern Asia. [*P. JAPONICUM* Maximowicz; *P. SACHALINENSE* (F. Schmidt) Sargent]

PTELEA TRIFOLIATA Linnaeus subsp. *TRIFOLIATA*—Common Hoptree (Figure 55). $2n = 42$. Woodland margins, roadsides, waste places. From farther south and west.

RUTA GRAVEOLENS Linnaeus—Common Rue (Figure 55). $2n = 72$, 76, 78, 80, 81. Waste places. From eastern Europe.

Zanthoxylum americanum Miller—Northern Prickly-Ash (Figure 55). $2n = 68$, 136. Thickets, rocky fields, rich woodlands, streambanks, meadows, roadsides.

SAPINDACEAE

ACER CAMPESTRE Linnaeus—Hedge Maple (Figure 55). $2n = 26$. Hedgerows, roadsides. From Eurasia, northwestern Africa.

ACER GINNALA Maximowicz—Amur Maple (Figure 55). $2n = 26$. Woodland and field margins, roadsides. From eastern Asia.

Acer negundo Linnaeus var. *negundo*—Ashleaf Maple (Figure 55). $2n = 26$. Roadsides, waste places, streambanks, alluvial woodlands, railroad margins.

ACER NEGUNDO Linnaeus var. *VIOLACEUM* Booth *ex* G. Kirchner—(Figure 55). $2n = ?$ Roadsides, waste places, woodland margins, streambanks. From farther west.

Acer nigrum F. Michaux—Black Maple (Figure 56). $2n = 26$. Rich, calcareous or alluvial woodlands.

Acer pensylvanicum Linnaeus—Striped Maple (Figure 56). $2n = 26$. Moist, rich woodlands.

ACER PLATANOIDES Linnaeus—Norway Maple (Figure 56). 2*n* = 26. Roadsides, hedgerows, waste places, woodland margins. From Eurasia.

ACER PSEUDOPLATANUS Linnaeus—Sycamore Maple (Figure 56). 2*n* = 52. Roadsides, fencerows, waste places, woodland margins, streambanks. From Eurasia.

Acer rubrum Linnaeus var. *rubrum*—Red Maple (Figure 56). 2*n* = 26. Acidic woodlands, swamps, alluvial soils, shores, moist fields.

Acer rubrum Linnaeus var. *trilobum* K. Koch—(Figure 56). 2*n* = ? Swamps, low woodlands.

Acer saccharinum Linnaeus—Silver Maple (Figure 56). 2*n* = 52. Streambanks, alluvial soils, swamps.

Acer saccharum Marshall—Sugar Maple (Figure 56). 2*n* = 26. Rich woodlands, especially in calcareous soils.

Acer spicatum Lamarck—Mountain Maple (Figure 56). 2*n* = 26. Rich, moist woodlands.

ACER TATARICUM Linnaeus—Tatarian Maple (Figure 57). 2*n* = 26. Roadsides. From Eurasia.

— *Acer* hybrid —

Acer × *freemanii* A.E. Murray—(Figure 57). [*A. rubrum* Linnaeus × *A. saccharinum* Linnaeus]

AESCULUS GLABRA Willdenow var. *GLABRA*—Ohio Buckeye (Figure 57). 2*n* = 40. Woodlands. From farther west and south.

AESCULUS HIPPOCASTANUM Linnaeus—Horse-chestnut (Figure 57). 2*n* = 40. Roadsides, waste places, woodland margins. From southeastern Europe.

SIMAROUBACEAE

AILANTHUS ALTISSIMA (Miller) Swingle—Tree-of-heaven (Figure 57). 2*n* = 80. Roadsides, waste places, woodland margins, fields. From China, Taiwan.

STAPHYLACEAE

Staphylea trifolia Linnaeus—American Bladdernut (Figure 57). 2*n* = 78. Rich woodland margins, thickets, roadsides.

VERBENACEAE

GLANDULARIA PULCHELLA (Sweet) Troncoso—(Figure 57). 2*n* = ? Waste places. From South America. [*VERBENA PULCHELLA* Sweet; *V. TENUISECTA* Briquet]

VERBENA BONARIENSIS Linnaeus—(Figure 57). $2n = 12, 14, 28$. Gravel pit. From South America. [*V. BONARIENSIS* var. *CONGLOMERATA* Briquet]

VERBENA BRACTEATA Lagasca & Rodríguez—(Figure 57). $2n = 14, 28$. Waste places, fields, roadsides, in open, sandy soils. From farther west.

Verbena hastata Linnaeus—Simpler's-joy (Figure 58). $2n = 14$. Wet thickets, shores, marshes, meadows, fields, roadsides.

VERBENA HISPIDA Ruiz & Pavón—(Figure 58). $2n = ?$ Waste places. From South America.

VERBENA OFFICINALIS Linnaeus—European Vervain (Figure 58). $2n = 14, 28, 42, 56$. Waste places. From Eurasia.

Verbena simplex Lehmann—(Figure 58). $2n = 14$. Dry fields, roadsides, railroads, rocky places, sandplains.

VERBENA STRICTA Ventenat—Hoary Vervain (Figure 58). $2n = 14$. Dry fields, roadsides, waste places. From farther west.

Verbena urticifolia Linnaeus—White Vervain (Figure 58). $2n = 14$. Rich thickets and woodland margins, alluvial soil, streambanks, meadows, fields, roadsides, waste places. [*V. urticifolia* var. *leiocarpa* L.M. Perry & Fernald]

— *Verbena* hybrids —

Verbena × *blanchardii* Moldenke—(Figure 58). [*V. hastata* Linnaeus × *V. simplex* Lehmann]

Verbena × *engelmanii* Moldenke—(Figure 58). [*V. hastata* Linnaeus × *V. urticifolia* Linnaeus]

VERBENA × *RYDBERGII* Moldenke—(Figure 58). [*V. hastata* Linnaeus × *V. STRICTA* Ventenat]

VISCACEAE

Arceuthobium pusillum Peck—Dwarf Mistletoe (Figure 59). $2n = 28$. Parasitic on *Picea*, rarely on *Larix* or *Pinus strobus*.

VITACEAE

AMPELOPSIS CORDATA Michaux—Raccoon-grape (Figure 59). $2n = 40$. Roadside thickets, salt marsh margins, sandy waste places. From farther south and west.

AMPELOPSIS GLANDULOSA (Wallich) Momiyama—Porcelain-berry (Figure 59). $2n = 20$. Roadsides, thickets, woodlands, waste places. From China. [*A. GLANDULOSA* var. *BREVIPEDUNCULATA* (Maximowicz) Momiyama; *A. BREVIPEDUNCULATA* (Maximowicz) Trautvetter]

Parthenocissus quinquefolia (Linnaeus) Planchon—Virginia-creeper (Figure 59). 2*n* = 40. Thickets, roadsides, woodlands, rocky banks, stone walls, fences. [*P. quinquefolia* var. *hirsuta* (Pursh) Planchon; *P. inserta* (A. Kerner) Fritsch]

PARTHENOCISSUS TRICUSPIDATA (Siebold & Zuccarini) Planchon—Boston Ivy (Figure 59). 2*n* = 40. Roadsides, fields, woodland margins, old walls. From eastern Asia.

Parthenocissus vitacea (Knerr) Hitchcock—Thicket-creeper (Figure 59). 2*n* = 40. Thickets, streambanks roadsides, woodlands, rocky banks. [*P. inserta* misapplied]

Vitis aestivalis Michaux—Summer Grape (Figure 59). 2*n* = 38. Open woodlands, thickets, roadsides, rocky outcrops and slopes. [*V. aestivalis* var. *argentifolia* (Munson *ex* L.H. Bailey) Fernald; *V. aestivalis* var. *bicolor* Deam]

Vitis labrusca Linnaeus—Fox Grape (Figure 59). 2*n* = 38. Thickets, streambanks, open woodlands, woodland and pond margins, roadsides.

VITIS PALMATA Vahl—Catbird Grape (Figure 59). 2*n* = 38. Railroads. From farther south and west.

Vitis riparia Michaux—Riverbank Grape (Figure 60). 2*n* = 38. Streambanks, alluvial woodlands, meadows, roadsides, rich thickets. [*V. riparia* var. *syrticola* (Fernald & Wiegand) Fernald; *V. VULPINA* misapplied]

VITIS VINIFERA Linnaeus—Wine Grape (Figure 60). 2*n* = 38, 40, 76. Waste places. From Eurasia, northwestern Africa.

VITIS VULPINA Linnaeus—Winter Grape (Figure 60). 2*n* = 38. Roadsides, thickets. From farther south and west.

— *Vitis* hybrids —

VITIS × *LABRUSCANA* L.H. Bailey—(Figure 60). [*V. labrusca* Linnaeus × *VITIS* spp.]

Vitis × *novae-angliae* Fernald (*pro species*)—(Figure 60). [*V. labrusca* Linnaeus × *V. riparia* Michaux]

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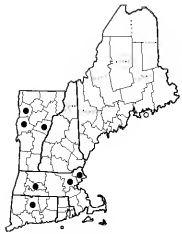
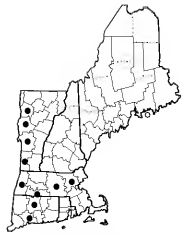
Figure 1 Key map for counties of the New England states (and Mt Desert Island, Maine; Block Island, Rhode Island; arbitrary divisions of larger Maine counties and of Coös County, New Hampshire)

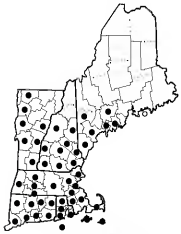
ACTINIDIA ARGUTA



COTINUS COGGYGRIA



Rhus aromatica
var. *aromatica*



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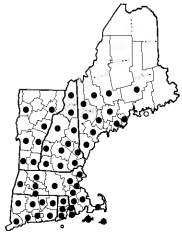

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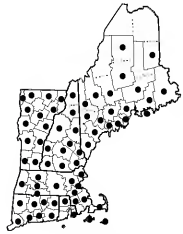

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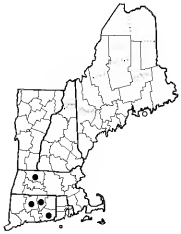

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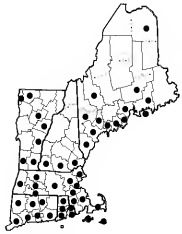
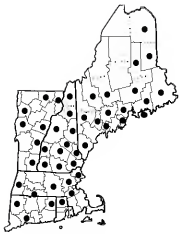


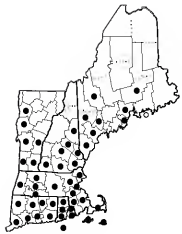
Toxicodendron radicans
subsp. *radicans*

Toxicodendron radicans
subsp. *negundo*

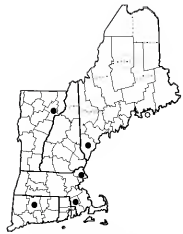
Figure 2. Distribution maps.



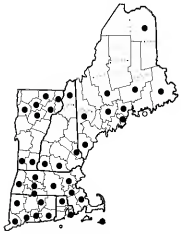
Toxicodendron rydbergii



Toxicodendron vernix

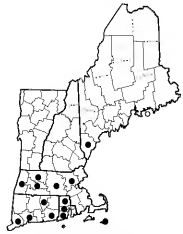


Toxicodendron radicans
X T. rydbergii

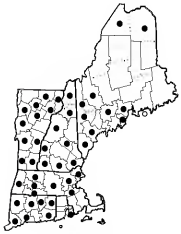


AEGOPODIUM PODAGRARIA

AETHUSA CYNAPIUM



ANETHUM GRAVEOLENS

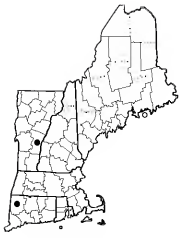


Angelica atropurpurea

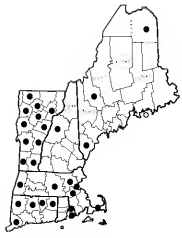
Angelica lucida

Angelica venenosa

Figure 3. Distribution maps.



ANTHRISCUS CEREFOLIUM

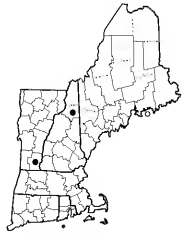


ANTHRISCUS SYLVESTRIS

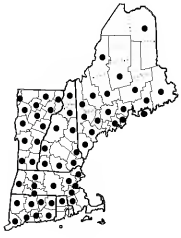
APIUM GRAVEOLENS var. *DULCE*

BIFORA RADIANS

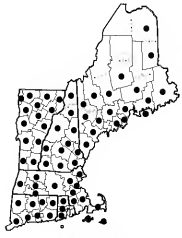
BUPLEURUM LANCIFOLIUM



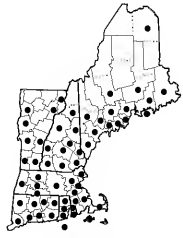
BUPLEURUM ROTUNDIFOLIUM



CARUM CARVI

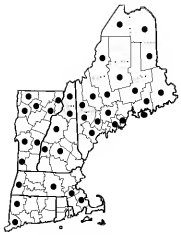


Cicuta bulbifera

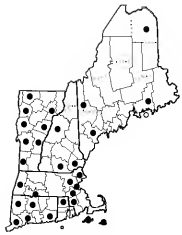


Cicuta maculata var. *maculata*

Figure 4. Distribution maps.

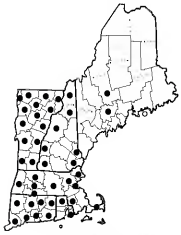


Conioselinum chinense

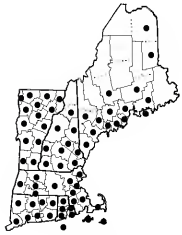


CONIUM MACULATUM

CORIANDRUM SATIVUM



Cryptotaenia canadensis



DAUCUS CAROTA

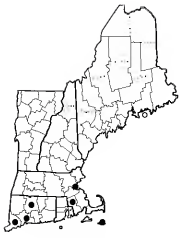
ERYNGIUM AMETHYSTINUM

ERYNGIUM PLANUM

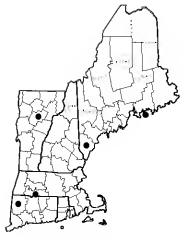
ERYNGIUM YUCCIFOLIUM
var. *YUCCIFOLIUM*

FALCARIA VULGARIS

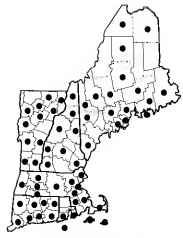
Figure 5. Distribution maps.



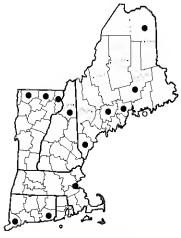
FOENICULUM VULGARE



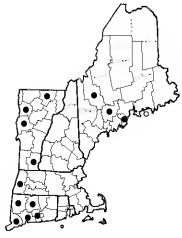
HERACLEUM MANTEGAZZIANUM



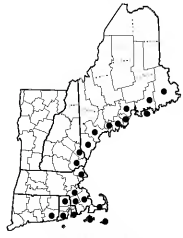
Heracleum sphondylium subsp. *montanum*



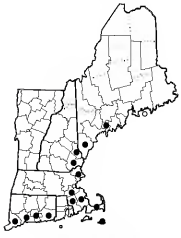
HERACLEUM SPHONDYLIUM subsp. *sibiricum*



LEVISTICUM OFFICINALE

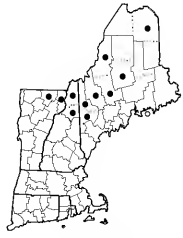


Ligusticum scoticum subsp. *scoticum*



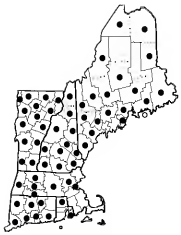
Lilaeopsis chinensis

MYRRHIS ODORATA



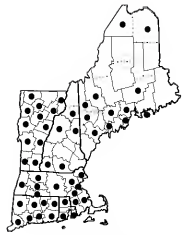
Osmorhiza berteroi

Figure 6. Distribution maps.

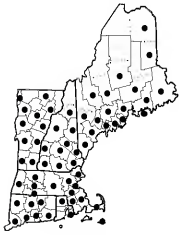


Osmorhiza claytonii

Osmorhiza depauperata

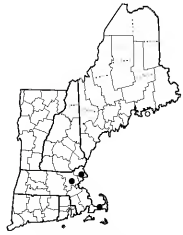


Osmorhiza longistylis



PASTINCA SATIVA

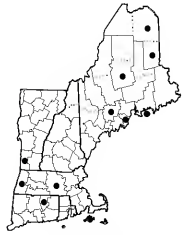
PETROSELINUM CRISPUM



PEUCEDANUM PALUSTRE

PIMPINELLA ANISUM

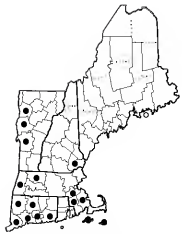
PIMPINELLA MAJOR



PIMPINELLA SAXIFRAGA
subsp. *SAXIFRAGA*

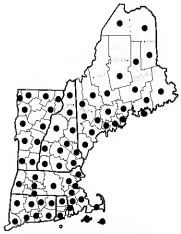
Figure 7. Distribution maps.

Ptilimnium capillaceum

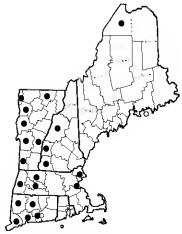


Sanicula canadensis var. *canadensis*

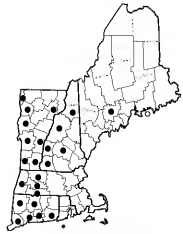
Sanicula canadensis var. *grandis*



Sanicula marilandica



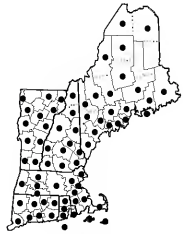
Sanicula odorata



Sanicula trifoliata

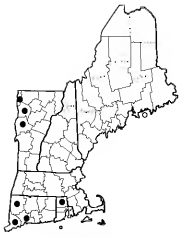
SCANDIX PECTEN-VENERIS

Sium carsonii



Sium suave

Figure 8. Distribution maps.



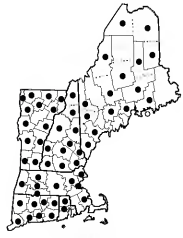
Taenidia integerrima

Thaspium trifoliatum var. *trifoliatum*

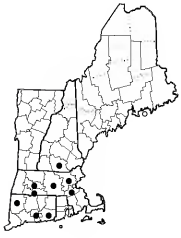
TORILIS JAPONICA

TORILIS LEPTOPHYLLA

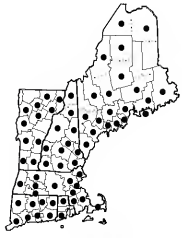
Zizia aptera



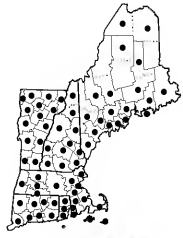
Zizia aurea



ARALIA ELATA

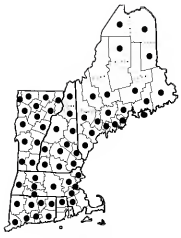


Aralia hispida



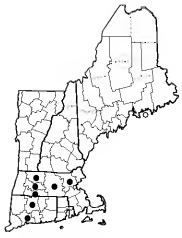
Aralia nudicaulis

Figure 9. Distribution maps.

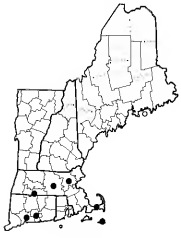


Aralia racemosa
subsp *racemosa*

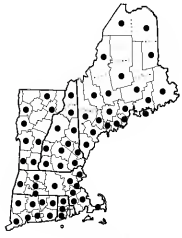
ARALIA SPINOSA



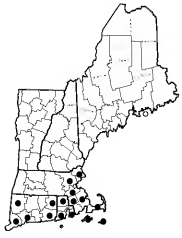
ELEUTHEROCOCCUS SIEBOLDIANUS



HEDERA HELIX



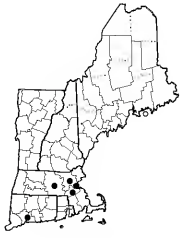
Hydrocotyle americana



Hydrocotyle umbellata

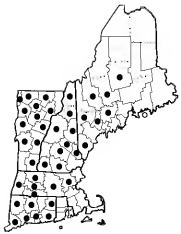
Hydrocotyle verticillata
var. *verticillata*

Hydrocotyle verticillata
var. *triradiata*

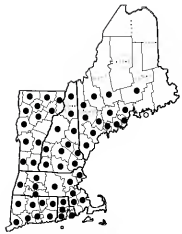


KALOPANAX SEPTEMLOBUS

Figure 10. Distribution maps.

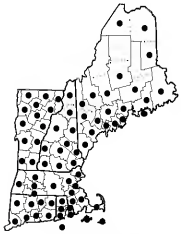


Panax quinquefolius

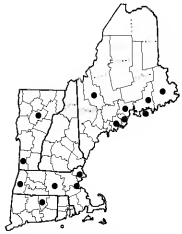


Panax trifolius

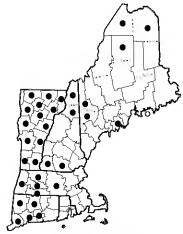
IMPATIENS BALSAMINA



Impatiens capensis



IMPATIENS GLANDULIFERA



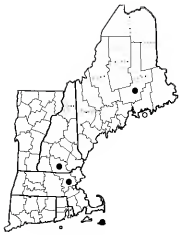
Impatiens pallida

AMSINCKIA EASTWOODIAE

AMSINCKIA INTERMEDIA

AMSINCKIA LYCOPSOIDES

Figure 11. Distribution maps.

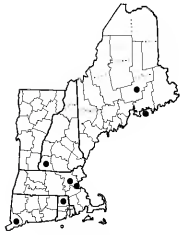


AMSINCKIA MENZIESII

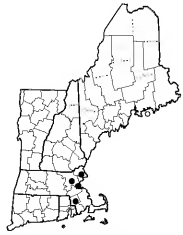
ANCHUSA ARVENSIS

ANCHUSA AZUREA

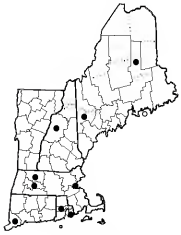
ANCHUSA LEPTOPHYLLA
subsp. *LEPTOPHYLLA*



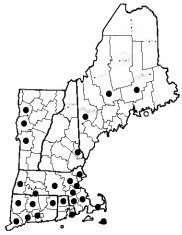
ANCHUSA OFFICINALIS



ASPERUGO PROCUMBENS



BORAGO OFFICINALIS



BUGLOSSOIDES ARVENSIS

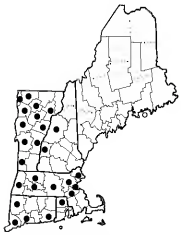
CRYPTANTHA AMBIGUA

Figure 12. Distribution maps.

CRYPTANTHA INTERMEDIA

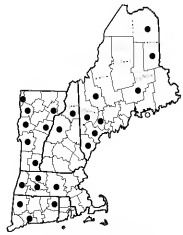
CYNOGLOSSUM AMABILE

CYNOGLOSSUM MICROGLOCHIN



CYNOGLOSSUM OFFICINALE

Cynoglossum virginianum var. *virginianum*



Cynoglossum virginianum var. *boreale*

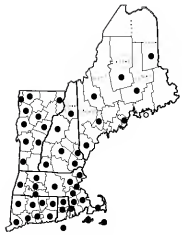
CYNOGLOTTIS BARRELIERI

ECHIUM CRETICUM

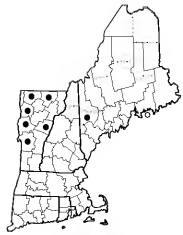
ECHIUM PLANTAGINEUM

Figure 13. Distribution maps.

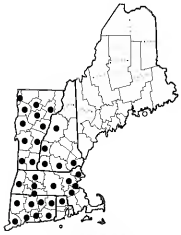
ECHIUM PUSTULATUM



ECHIUM VULGARE



Hackelia deflexa var. *americana*



Hackelia virginiana

HELIOTROPIUM AMPLEXICAULE

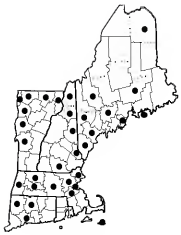
HELIOTROPIUM CURASSIVICUM var. *CURASSAVICUM*

HELIOTROPIUM EUROPAEUM

HELIOTROPIUM INDICUM

LAPPULA OCCIDENTALIS var. *OCCIDENTALIS*

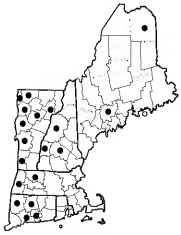
Figure 14. Distribution maps.



LAPPULA SQUARROSA

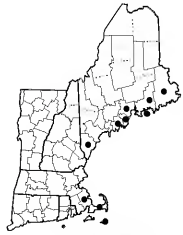
LITHOSPERMUM CANESCENS

LITHOSPERMUM OCCIDENTALE



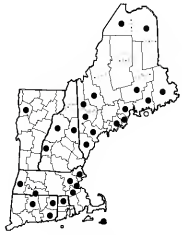
LITHOSPERMUM OFFICINALE

Lithospermum virginianum

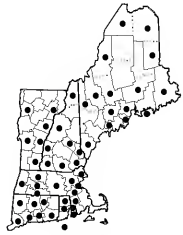


Mertensia maritima
subsp. *tenella*

MERTENSIA VIRGINICA

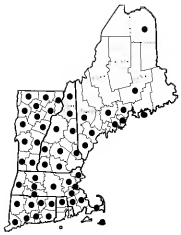


MYOSOTIS ARVENSIS

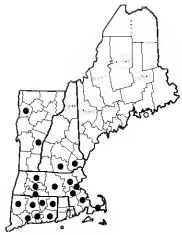


Myosotis laxa

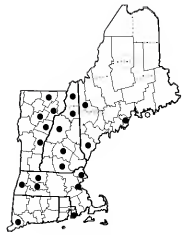
Figure 15. Distribution maps.



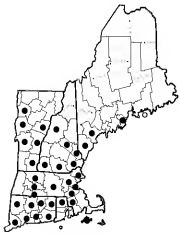
MYOSOTIS SCORPIOIDES



MYOSOTIS STRICTA



MYOSOTIS SYLVATICA



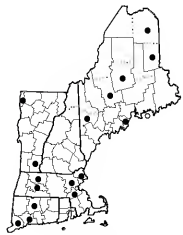
Myosotis verna

NONEA ROSEA

PENTAGLOTTIS SEMPERVIRENS

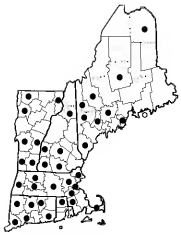
PLAGIOBOTHRYS RETICULATUS

PULMONARIA SACCHARATA



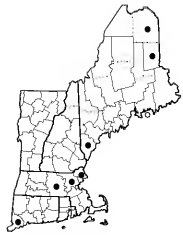
SYMPHYTUM ASPERUM

Figure 16. Distribution maps.

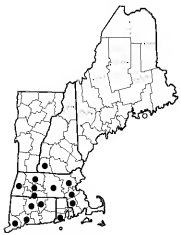


SYMPHYTUM OFFICINALE

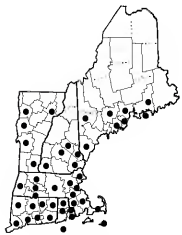
SYMPHYTUM TUBEROSUM



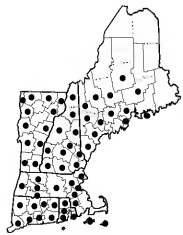
SYMPHYTUM X UPLANDICUM



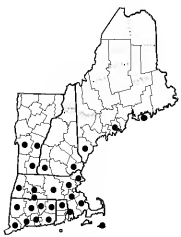
PACHYSANDRA TERMINALIS



CELASTRUS ORBICULATUS

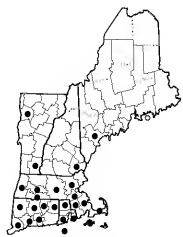


Celastrus scandens



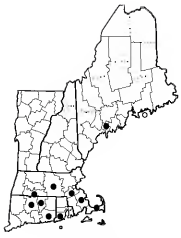
EUONYMUS ALATUS

EUONYMUS ATROPURPUREUS
var. *ATROPURPUREUS*



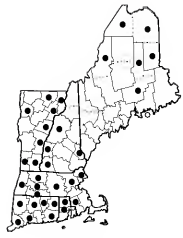
EUONYMUS EUROPAEUS

Figure 17. Distribution maps.

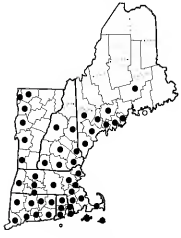


EUONYMUS FORTUNEI
var *FORTUNEI*

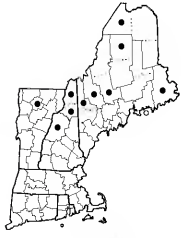
EUONYMUS FORTUNEI
var *RADICANS*



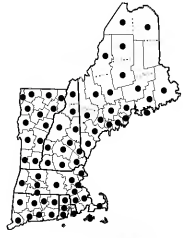
Parnassia glauca



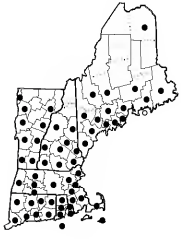
Comandra umbellata
subsp *umbellata*



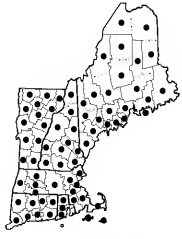
Geocaulon lividum



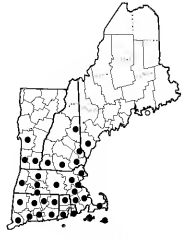
Cornus alternifolia



Cornus amomum

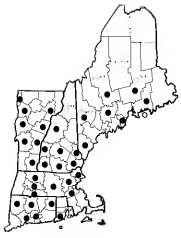


Cornus canadensis

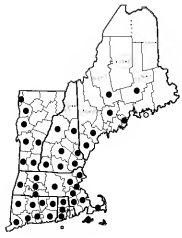


Cornus florida

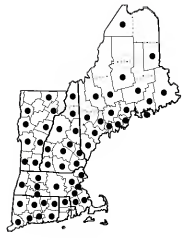
Figure 18. Distribution maps.



Cornus obliqua

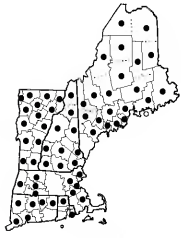


Cornus racemosa



Cornus rugosa

CORNUS SANGUINEA



Cornus stolonifera

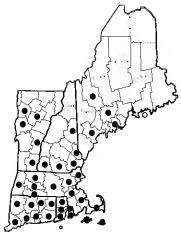
Cornus X arnoldiana

Cornus X slavinii

ELAEAGNUS ANGUSTIFOLIA

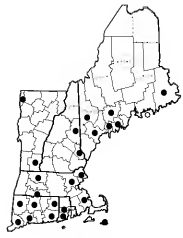
ELAEAGNUS MULTIFLORA

Figure 19. Distribution maps.

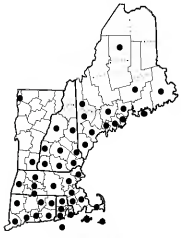


ELAEAGNUS UMBELLATA
var. *PARVIFLORA*

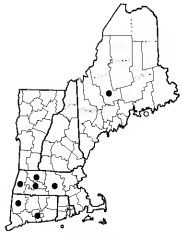
Shepherdia canadensis



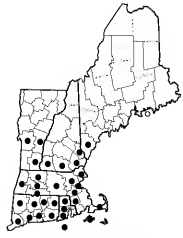
Elatine americana



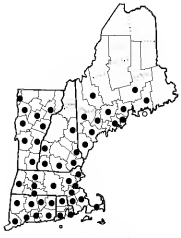
Elatine minima



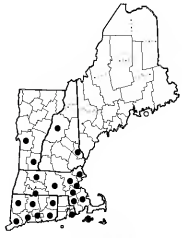
ELATINE TRIANDRA



Acalypha gracilens



Acalypha rhomboidea



Acalypha virginica

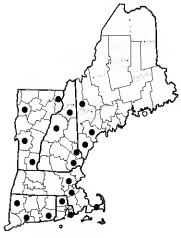
CROTON CAPITATUS

Figure 20. Distribution maps.

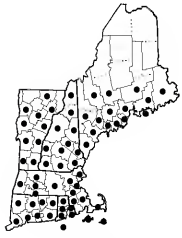
CROTON GLANDULOSUS
var. *SEPTENTRIONALIS*

CROTON MICHAUXII
var. *ELLIPTICA*

CROTON TEXENSIS

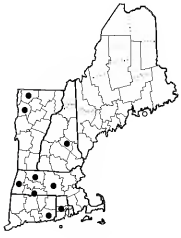


EUPHORBIA COROLLATA



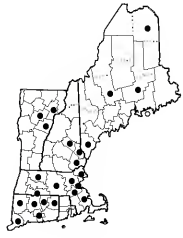
EUPHORBIA CYPARISSIAS

EUPHORBIA DAVIDII



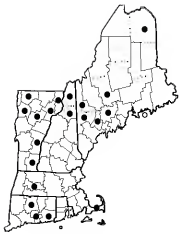
EUPHORBIA DENTATA

EUPHORBIA DULCIS

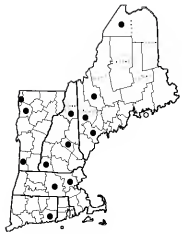


EUPHORBIA ESULA

Figure 21. Distribution maps.

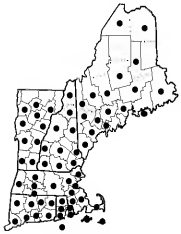


Euphorbia glyptosperma



EUPHORBIA HELIOSCOPIA

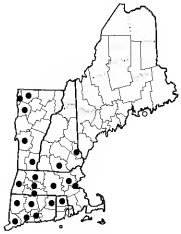
EUPHORBIA LATHYRIS



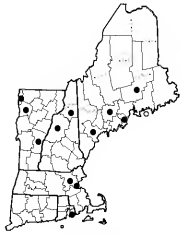
Euphorbia maculata

EUPHORBIA MARGINATA

EUPHORBIA MESEMBRIANTHEMIFOLIA



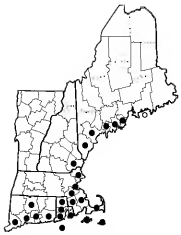
Euphorbia nutans



EUPHORBIA PEPLUS

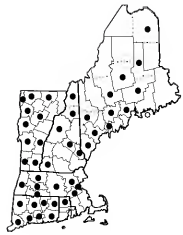
EUPHORBIA PLATYPHYLLOS

Figure 22. Distribution maps.

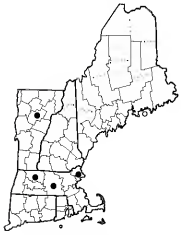


Euphorbia polygonifolia

EUPHORBIA PROSTRATA

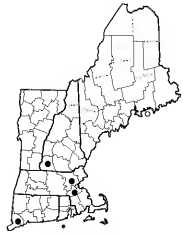


Euphorbia vermiculata

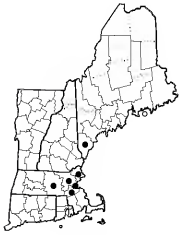


EUPHORBIA X PSEUDOESULA

MERCURIALIS ANNUA



RICINUS COMMUNIS

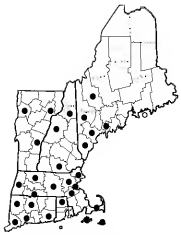


ERODIUM BOTRYS

ERODIUM BRACHYCARPUM

ERODIUM CICONIUM

Figure 23. Distribution maps.



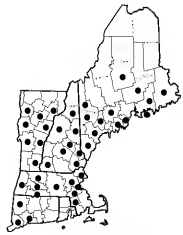
ERODIUM CICUTARIUM
subsp. *CICUTARIUM*

ERODIUM CYGNORUM

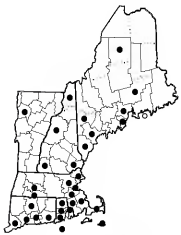
ERODIUM MALACOIDES

ERODIUM MOSCHATUM

ERODIUM STEPHANIANUM



Geranium bicknellii



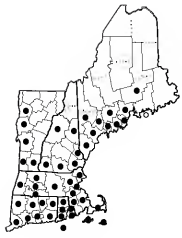
Geranium carolinianum
var. *carolinianum*

GERANIUM COLUMBINUM

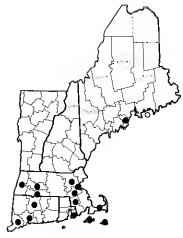
GERANIUM DISSECTUM

Figure 24. Distribution maps.

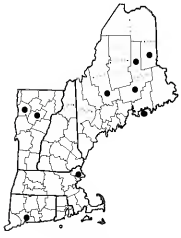
GERANIUM ERIANTHUM



Geranium maculatum



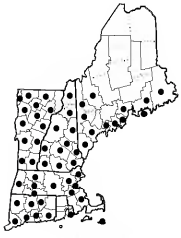
GERANIUM MOLLE



GERANIUM PRATENSE

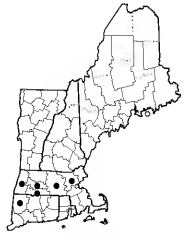
GERANIUM PUSILLUM

GERANIUM PYRENAICUM



Geranium robertianum

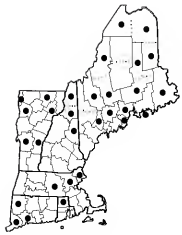
GERANIUM SANGUINEUM



GERANIUM SIBIRICUM

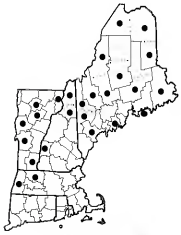
Figure 25. Distribution maps.

GERANIUM THUNBERGII

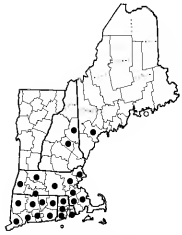


Myriophyllum alterniflorum

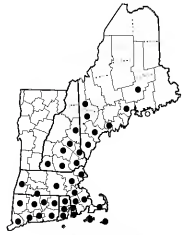
MYRIOPHYLLUM AQUATICUM



Myriophyllum farwellii

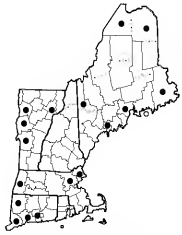


MYRIOPHYLLUM HETEROPHYLLUM

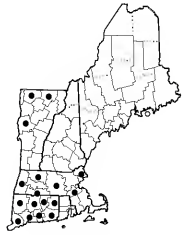


Myriophyllum humile

Myriophyllum pinnatum

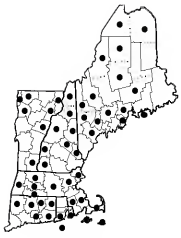


Myriophyllum sibiricum

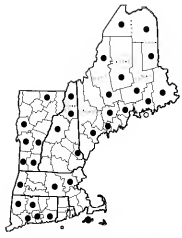


MYRIOPHYLLUM SPICATUM

Figure 26. Distribution maps.



Myriophyllum tenellum

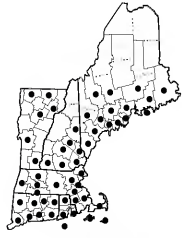


Myriophyllum verticillatum

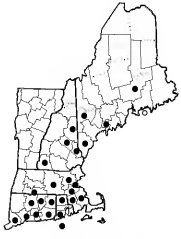
MYRIPHYLLUM HETEROPHYLLUM X M. LAXUM

MYRIPHYLLUM HETEROPHYLLUM X M. pinnatum

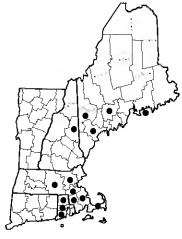
Proserpinaca intermedia



Proserpinaca palustris var. palustris



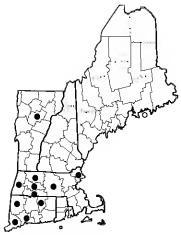
Proserpinaca palustris var. crebra



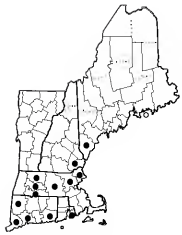
Proserpinaca pectinata

DEUTZIA SCABRA

Figure 27. Distribution maps.



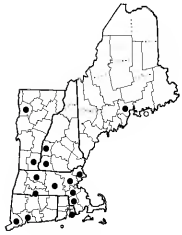
HYDRANGEA ARBORESCENS



HYDRANGEA PANICULATA

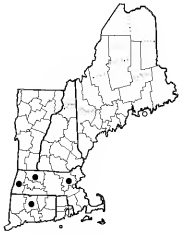
HYDRANGEA QUERCIFOLIA

HYDRANGEA RADIATA

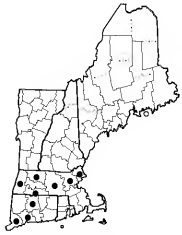


PHILADELPHUS CORONARIUS

PHILADELPHUS INCANUS



PHILADELPHUS INODORUS



PHILADELPHUS PUBESCENS

PHILADELPHUS X NIVALIS

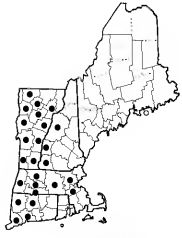
Figure 28. Distribution maps.

PHILADELPHUS X POLYANTHUS

PHILADELPHUS X VIRGINALIS

ELLISIA NYCTELEA

Hydrophyllum canadense



Hydrophyllum virginianum var. *virginianum*

PHACELIA BRACHYLOBA

PHACELIA DISTANS

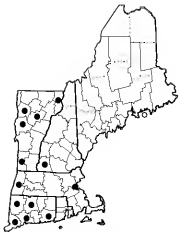
PHACELIA EGENA

PHACELIA MINOR

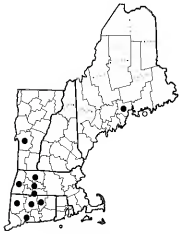
Figure 29. Distribution maps.

AGASTACHE FOENICULUM

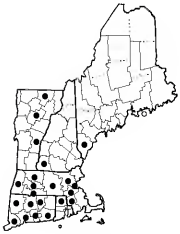
Agastache nepetoides



Agastache scrophulariifolia

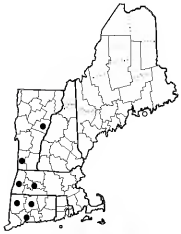


AJUGA GENEVENSIS

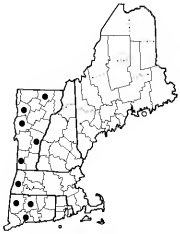


AJUGA REPTANS

BALLOTA NIGRA
var. *NIGRA*



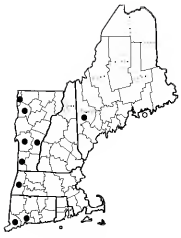
Blephilia ciliata



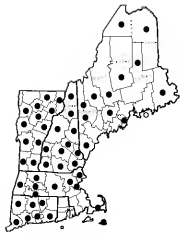
Blephilia hirsuta
var. *hirsuta*

Blephilia hirsuta
var. *glabrata*

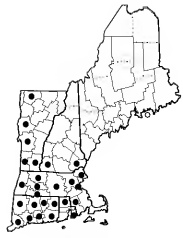
Figure 30. Distribution maps.



CLINOPODIUM ACINOS

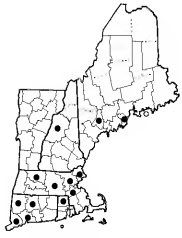


Clinopodium vulgare

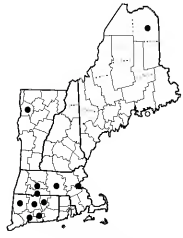


Collinsonia canadensis

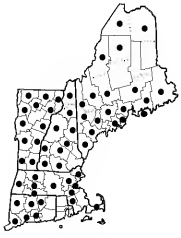
DRACOCEPHALUM MOLDAVICA



DRACOCEPHALUM PARVIFLORUM

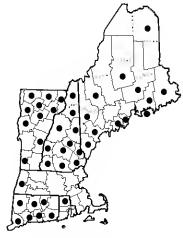


ELSHOLTZIA CILIATA



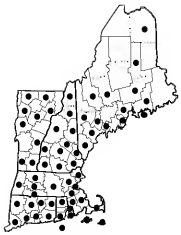
GALEOPSIS BIFIDA

GALEOPSIS LADANUM
var. *LADANUM*

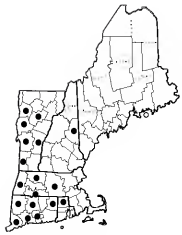


GALEOPSIS TETRAHIT

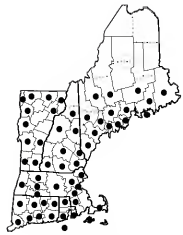
Figure 31. Distribution maps.



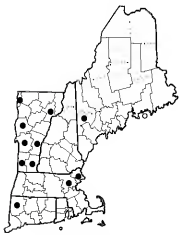
GLECHOMA HEDERACEA



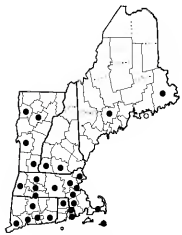
HEDEOMA HISPIDA



Hedeoma pulegioides

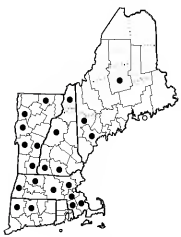


HYSSOPUS OFFICINALIS

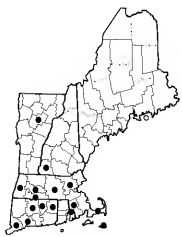


LAMIUM AMPLEXICAULE

LAMIUM GALEOBDOLON



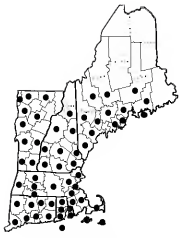
LAMIUM MACULATUM



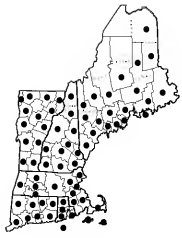
LAMIUM PURPUREUM
var. *PURPUREUM*

LAMIUM PURPUREUM
var. *INCISUM*

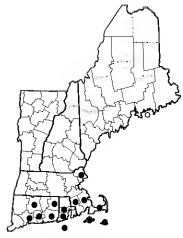
Figure 32. Distribution maps.



LEONURUS CARDIACA subsp *CARDIACA*



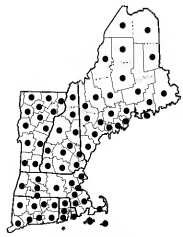
Lycopus americanus



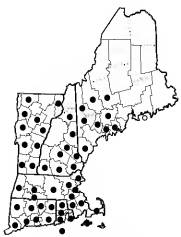
Lycopus amplectens

LYCOPUS EUROPAEUS

Lycopus rubellus



Lycopus uniflorus var. *uniflorus*

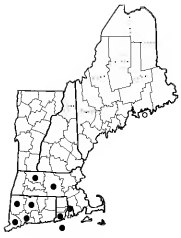


Lycopus virginicus

Lycopus X sherardii

MARRUBIUM VULGARE

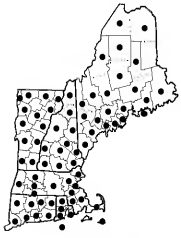
Figure 33. Distribution maps.



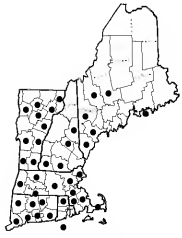
MELISSA OFFICINALIS

MENTHA AQUATICA
var *CITRATA*

MENTHA ARVENSIS
subsp *PARIETARIIFOLIA*

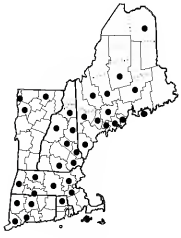


Mentha canadensis

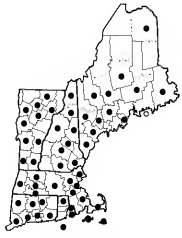


MENTHA SPICATA
var *SPICATA*

MENTHA SUAVEOLENS
subsp *SUAVEOLENS*



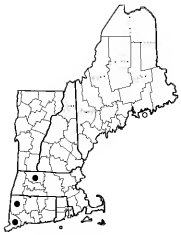
MENTHA X GRACILIS



MENTHA X PIPERITA

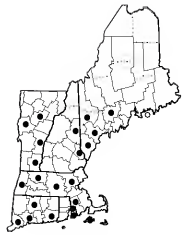
MENTHA X ROTUNDIFOLIA

Figure 34. Distribution maps



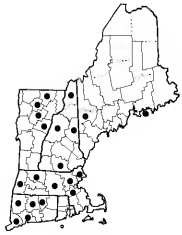
MENTHA X SMITHIANA

MENTHA X VERTICILLATA

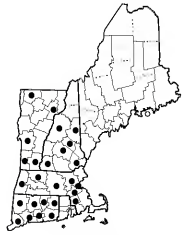


MENTHA X VILLOSA

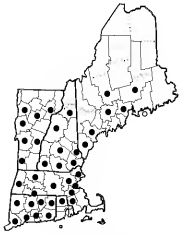
MONARDA CLINOPODIA



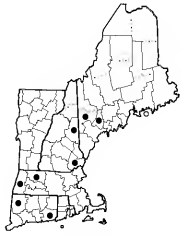
MONARDA DIDYMA



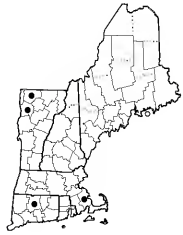
Monarda fistulosa
var. *fistulosa*



Monarda fistulosa
var. *mollis*

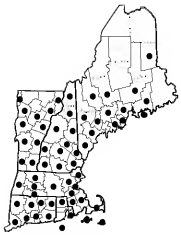


MONARDA MEDIA



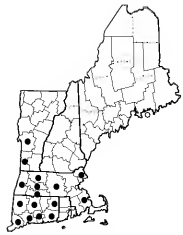
Monarda punctata
var. *villicaulis*

Figure 35. Distribution maps.



NEPETA CATARIA

OCIMUM BASILICUM

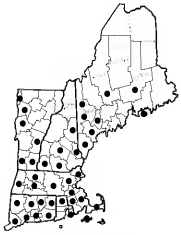


ORIGANUM VULGARE
subsp. *VULGARE*

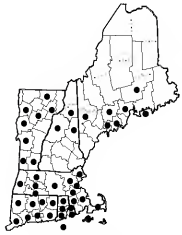
PERILLA FRUTESCENS
var. *FRUTESCENS*

PERILLA FRUTESCENS
var. *CRISPA*

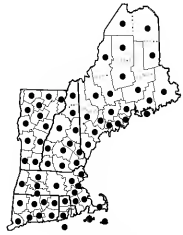
PEROVSKIA ATRICIPLICIFOLIA



Physostegia virginiana
subsp. *virginiana*

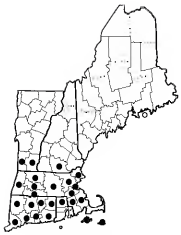


PRUNELLA VULGARIS
subsp. *VULGARIS*

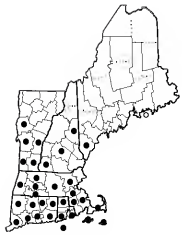


Prunella vulgaris
subsp. *lanceolata*

Figure 36. Distribution maps.

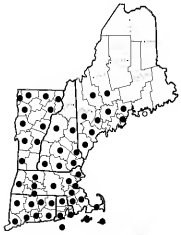


Pycnanthemum incanum
var. *incanum*



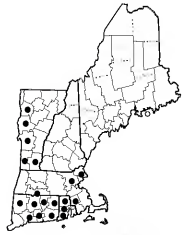
Pycnanthemum muticum

PYCNANTHEMUM PILOSUM

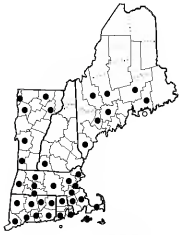


Pycnanthemum tenuifolium

Pycnanthemum torreyi



Pycnanthemum verticillatum



Pycnanthemum virginianum

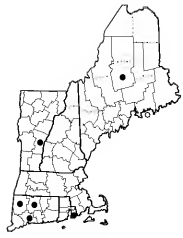
Pycnanthemum X *clinopodioides*

SALVIA AZUREA
var. *GRANDIFLORA*

Figure 37. Distribution maps.

SALVIA FARINACEA

Salvia lyrata



SALVIA OFFICINALIS

SALVIA PRATENSIS

SALVIA SCLAREA

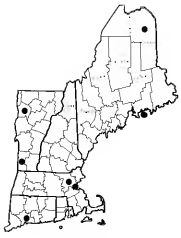
SALVIA SPLENDENS

SALVIA SYLVESTRIS

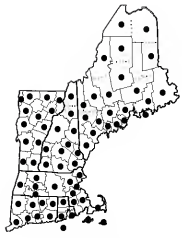
SALVIA TILIIFOLIA

SALVIA VERTICILLATA

Figure 38. Distribution maps.

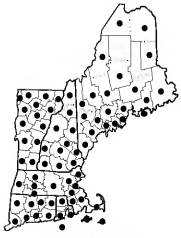


SATUREJA HORTENSIS



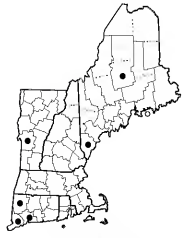
Scutellaria galericulata

Scutellaria integrifolia

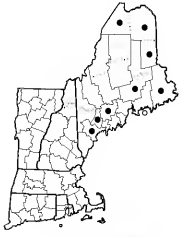


Scutellaria lateriflora
var. *lateriflora*

Scutellaria parvula
var. *parvula*



Scutellaria parvula
var. *missouriensis*

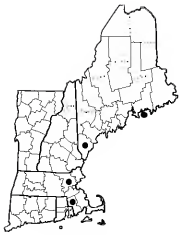


Scutellaria X churchilliana

SIDERITIS MONTANA

STACHYS ANNUA

Figure 39. Distribution maps.

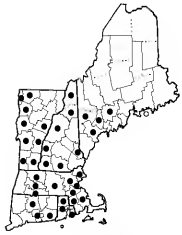


STACHYS ARVENSIS

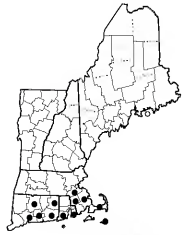
STACHYS ASPERA

STACHYS BYZANTINA

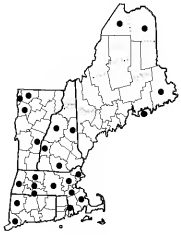
STACHYS GERMANICA



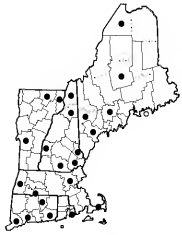
Stachys hispida



Stachys hyssopifolia



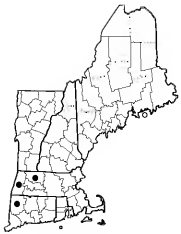
STACHYS PALUSTRIS



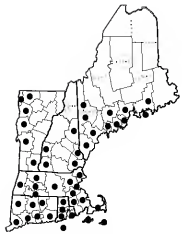
Stachys pilosa
var. *pilosa*

STACHYS PILOSA
var. *ARENICOLA*

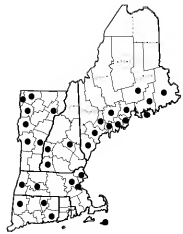
Figure 40. Distribution maps.



TEUCRIUM BOTRYS

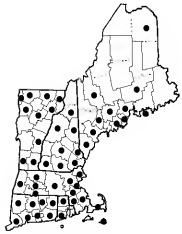


Teucrum canadense
var *canadense*

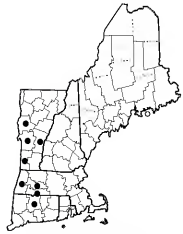


Teucrum canadense
var *occidentale*

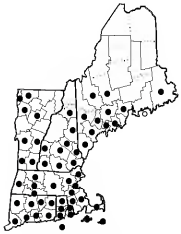
TEUCRIUM SCORODONIA



THYMUS PULEGIOIDES

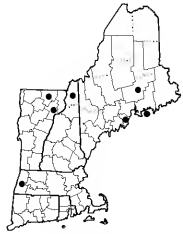


Trichostema brachiatum



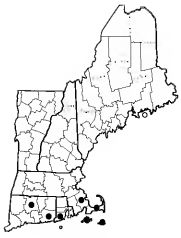
Trichostema dichotomum

Trichostema setaceum

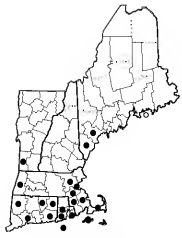


LINUM CATHARTICUM

Figure 41. Distribution maps.



Linum intercursum

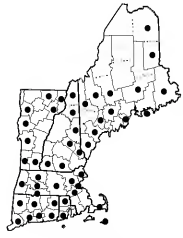


Linum medium
var. *texanum*

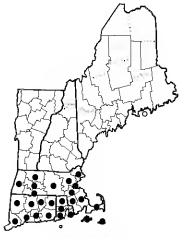
LINUM PERENNE

Linum striatum

Linum sulcatum



LINUM USITATISSIMUM



Linum virginianum

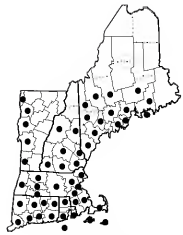
RADIOLA LINOIDES

MENTZELIA OLIGOSPERMA

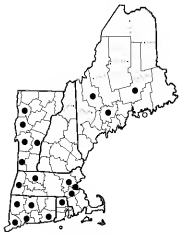
Figure 42. Distribution maps.

CUPHEA PROCUMBENS

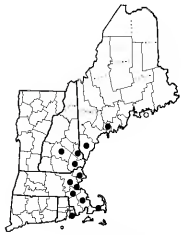
Cuphea viscosissima



Decodon verticillatus

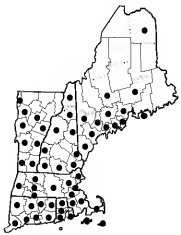


LYTHRUM ALATUM
var. *ALATUM*



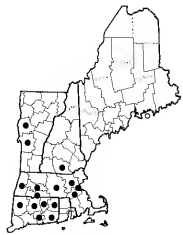
Lythrum hyssopifolia

LYTHRUM JUNCEUM



LYTHRUM SALICARIA

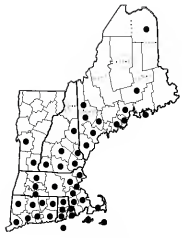
Rotala ramosior



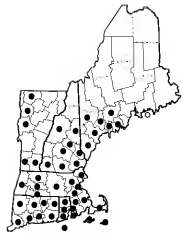
TRAPA NATANS

Figure 43. Distribution maps.

Rhexia mariana var. mariana

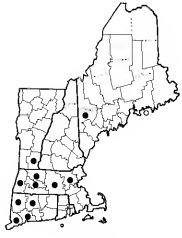


Rhexia virginica



Nyssa sylvatica

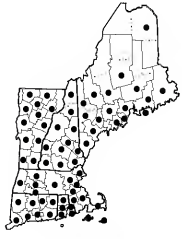
CHIONANTHUS VIRGINICUS



FORSYTHIA SUSPENSA

FORSYTHIA VIRIDISSIMA

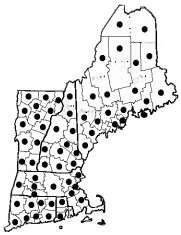
FORSYTHIA X INTERMEDIA



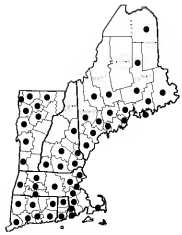
Fraxinus americana

FRAXINUS EXCELSIOR

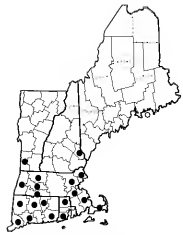
Figure 44. Distribution maps.



Fraxinus nigra



Fraxinus pennsylvanica

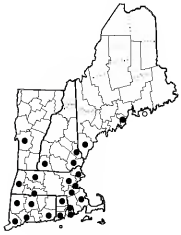


LIGUSTRUM OBTUSIFOLIUM subsp. *OBTUSIFOLIUM*

LIGUSTRUM OBTUSIFOLIUM subsp. *SUAVE*

LIGUSTRUM OVALIFOLIUM

LIGUSTRUM SINENSE

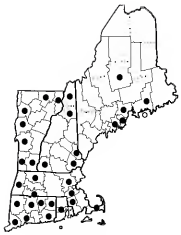


LIGUSTRUM VULGARE

SYRINGA RETICULATA subsp. *RETICULATA*

SYRINGA VILLOSA

Figure 45. Distribution maps.



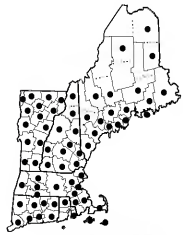
SYRINGA VULGARIS

SYRINGA X CHINENSIS

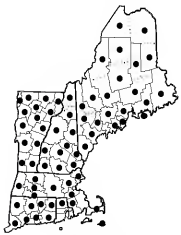
SYRINGA X PERSICA

CAMISSONIA CAMPESTRIS
subsp. *CAMPESTRIS*

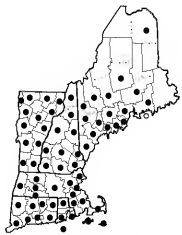
CAMISSONIOPSIS BISTORTA



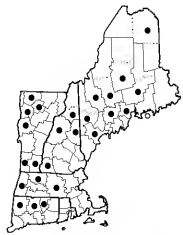
Chamaenerion angustifolium
subsp. *circumvagum*



Circaea alpina
subsp. *alpina*



Circaea canadensis

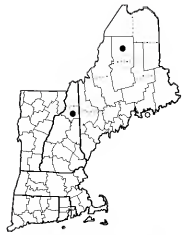


Circaea X sterilis

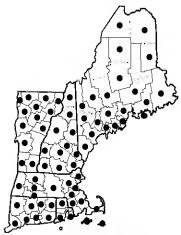
Figure 46. Distribution maps.

CLARKIA PULCHELLA

CLARKIA RHOMBOIDEA

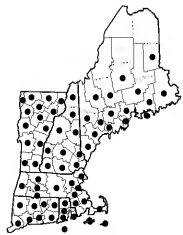


Epilobium anagallidifolium

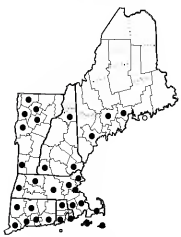


Epilobium ciliatum
subsp. *ciliatum*

Epilobium ciliatum
subsp. *glandulosum*



Epilobium coloratum

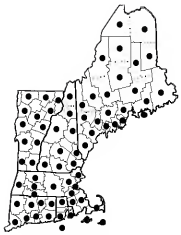


EPILOBIUM HIRSUTUM

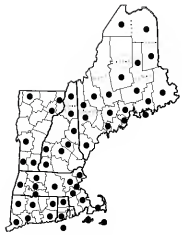
Epilobium hornemannii
subsp. *hornemannii*

Epilobium lactiflorum

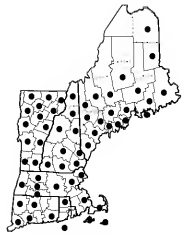
Figure 47. Distribution maps.



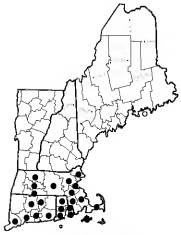
Epilobium leptophyllum



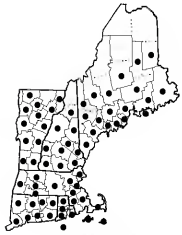
Epilobium palustre



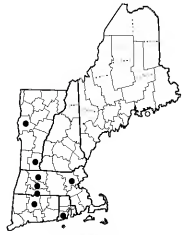
Epilobium strictum



Ludwigia alternifolia



Ludwigia palustris



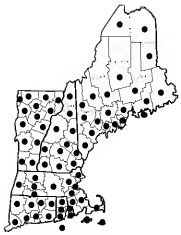
Ludwigia polycarpa

Ludwigia sphaerocarpa

Ludwigia X lacustris

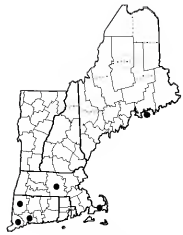
OENOTHERA AFFINIS

Figure 48. Distribution maps.

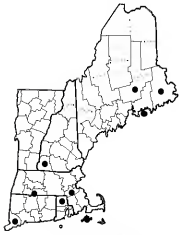


Oenothera biennis

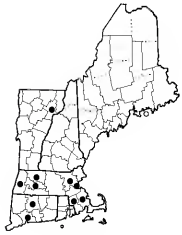
OENOTHERA CURTIFLORA



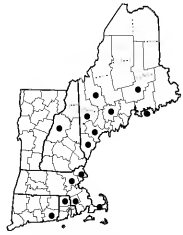
Oenothera fruticosa subsp. *fruticosa*



Oenothera fruticosa subsp. *tetragona*



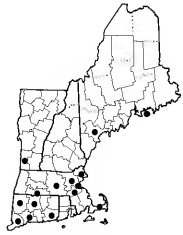
OENOTHERA GAURA



OENOTHERA GLAZIOVIANA

OENOTHERA GRANDIFLORA

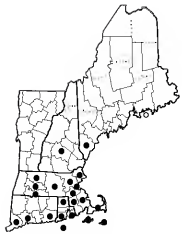
OENOTHERA GRANDIS



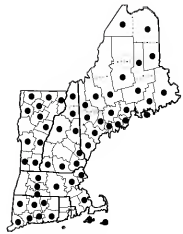
OENOTHERA LACINIATA

Figure 49. Distribution maps.

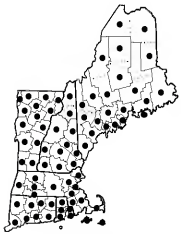
Oenothera nutans



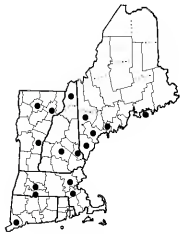
Oenothera oakesiana



Oenothera parviflora



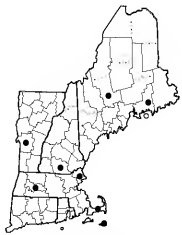
Oenothera perennis



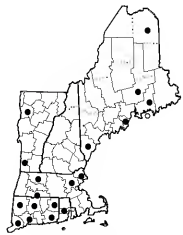
OENOTHERA PILOSELLA

OENOTHERA SERRULATA

OENOTHERA SPECIOSA

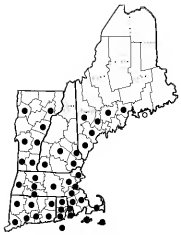


OENOTHERA VILLOSA
subsp. *VILLOSA*

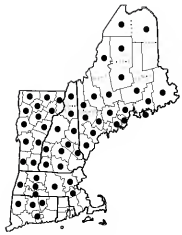


OXALIS CORNICULATA

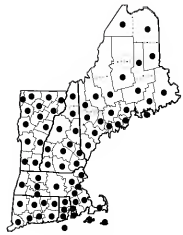
Figure 50. Distribution maps.



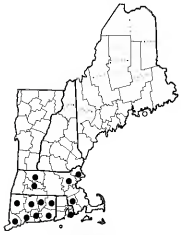
Oxalis dillenii



Oxalis montana

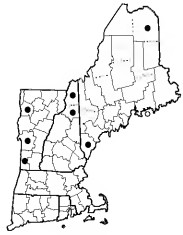


Oxalis stricta



Oxalis violacea

Oxalis dillenii
X *O. stricta*



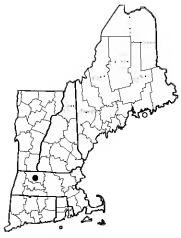
COLLOMIA LINEARIS

GILIA ACHILLEIFOLIA
subsp. *MULTICAULIS*

GILIA INTERIOR

GILIA TRICOLOR
subsp. *DIFFUSA*

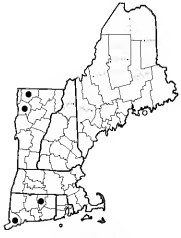
Figure 51. Distribution maps.



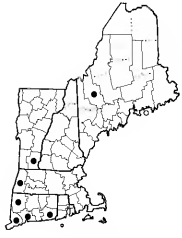
IPOMOPSIS RUBRA

NAVARRETIA LEUCOCEPHALA
subsp. *MINIMA*

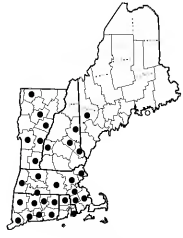
PHLOX BIFIDA
subsp. *BIFIDA*



Phlox divaricata
subsp. *divaricata*

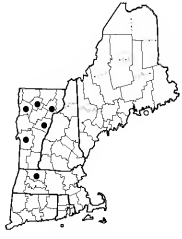


Phlox maculata
subsp. *maculata*

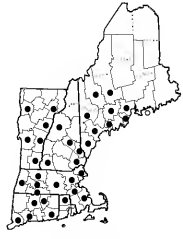


PHLOX PANICULATA

Phlox pilosa
subsp. *pilosa*



PHLOX STOLONIFERA

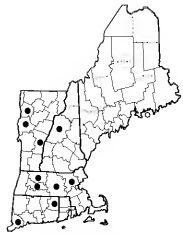


PHLOX SUBULATA
subsp. *SUBULATA*

Figure 52. Distribution maps.

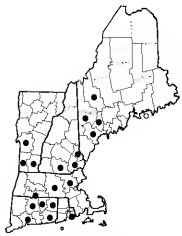
PHLOX X PROCUMBENS

POLEMONIUM CAERULEUM
subsp *CAERULEUM*

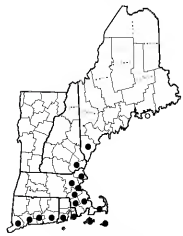


POLEMONIUM REPTANS
subsp *REPTANS*

Polemonium vanbruntiae

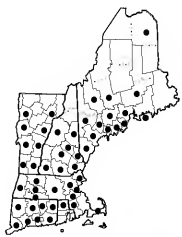


Polygala ambigua

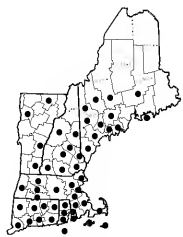


Polygala cruciata
var *aquiloma*

Polygala nuttallii

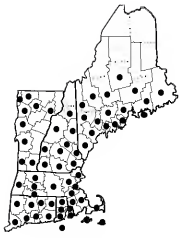


Polygala paucifolia

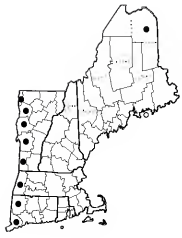


Polygala polygama

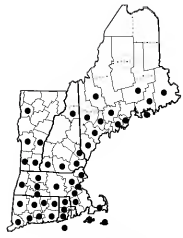
Figure 53. Distribution maps.



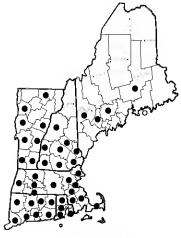
Polygala sanguinea



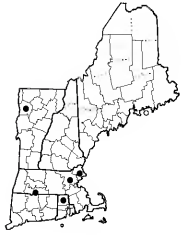
Polygala senega



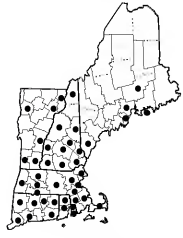
Polygala verticillata var *verticillata*



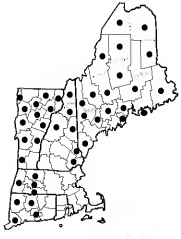
Ceanothus americanus



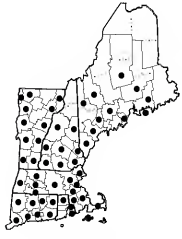
Ceanothus herbaceus



FRANGULA ALNUS



Rhamnus alnifolia

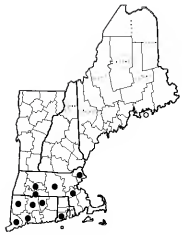


RHAMNUS CATHARTICA

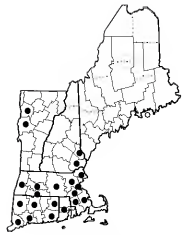
RHAMNUS DAVURICA subsp. *DAVURICA*

Figure 54. Distribution maps.

DICTAMNUS ALBUS

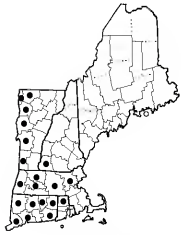


PHELLODENDRON AMURENSE



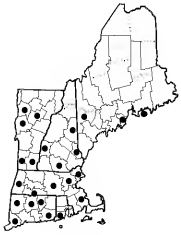
PTELEA TRIFOLIATA
subsp. *TRIFOLIATA*

RUTA GRAVEOLENS

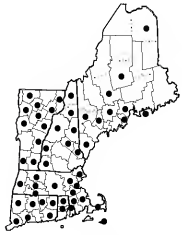


Zanthoxylum americanum

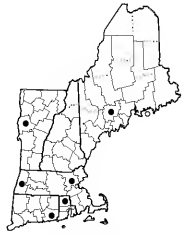
ACER CAMPESTRE



ACER GINNALA

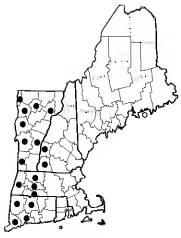


Acer negundo
var. *negundo*

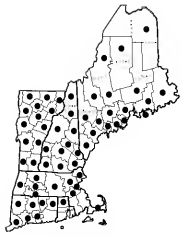


ACER NEGUNDO
var. *VIOLACEUM*

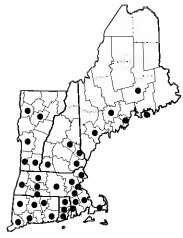
Figure 55. Distribution maps.



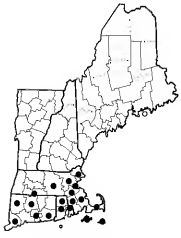
Acer nigrum



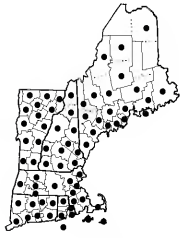
Acer pensylvanicum



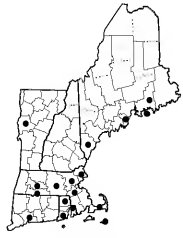
ACER PLATANOIDES



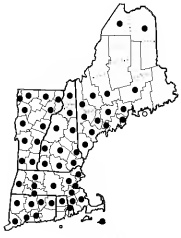
ACER PSEUDOPLATANUS



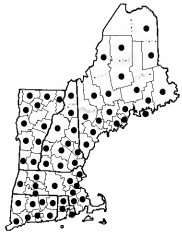
Acer rubrum
var. *rubrum*



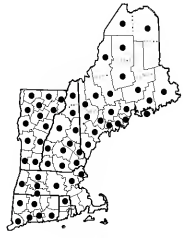
Acer rubrum
var. *trilobum*



Acer saccharinum



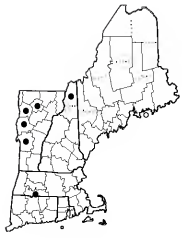
Acer saccharum
var. *saccharum*



Acer spicatum

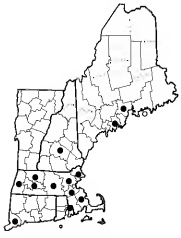
Figure 56. Distribution maps.

ACER TATARICUM

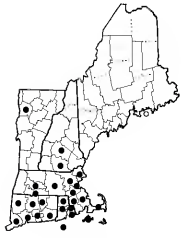


Acer X freemanii

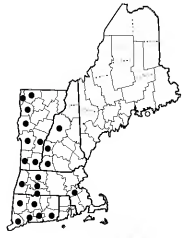
AESCULUS GLABRA
var. *GLABRA*



AESCULUS HIPPOCASTANUM



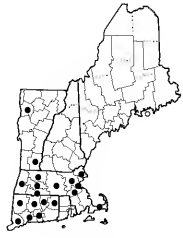
AILANTHUS ALTISSIMA



Staphylea trifolia

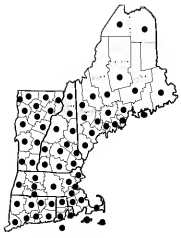
GLANDULARIA PULCHELLA

VERBENA BONARIENSIS



VERBENA BRACTEATA

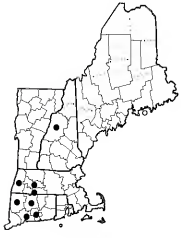
Figure 57. Distribution maps.



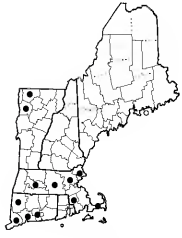
Verbena hastata

VERBENA HISPIDA

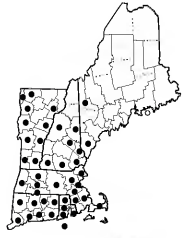
VERBENA OFFICINALIS



Verbena simplex



VERBENA STRICTA



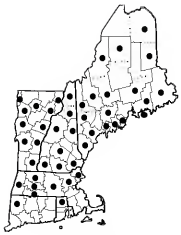
Verbena urticifolia

Verbena X blanchardii

Verbena X engelmannii

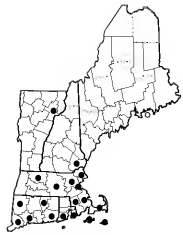
VERBENA X RYDBERGII

Figure 58. Distribution maps.

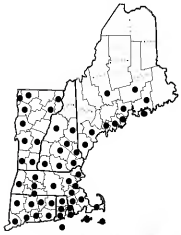


Arceuthobium pusillum

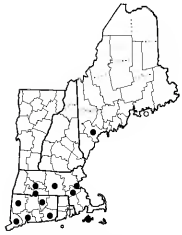
AMPELOPSIS CORDATA



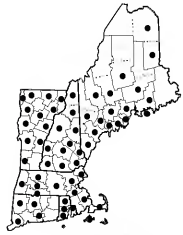
AMPELOPSIS GLANDULOSA



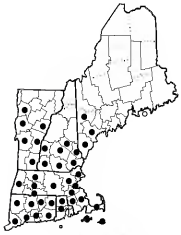
Parthenocissus quinquefolia



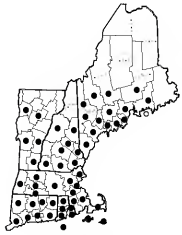
PARTHENOCISSUS TRICUSPIDATA



Parthenocissus vitacea



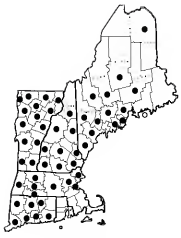
Vitis aestivalis



Vitis labrusca

VITIS PALMATA

Figure 59. Distribution maps.

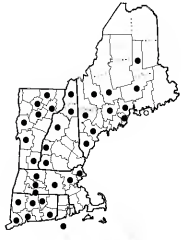


Vitis riparia

VITIS VINIFERA

VITIS VULPINA

VITIS X LABRUSCANA



Vitis X novae-angliae

Figure 60. Distribution maps.

Guillén Rodríguez, Y. and G. Vargas . 2014. *Voyria crucitasensis* (Gentianaceae), una nueva especie de planta micoheterotrófica para Costa Rica. Phytoneuron 2014-99: 1–6. Published 14 October 2014. ISSN 2153 733X

VOYRIA CRUCITASENSIS (GENTIANACEAE), UNA NUEVA ESPECIE DE PLANTA MICOHETEROTRÓFICA PARA COSTA RICA

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ABSTRACT

Voyria crucitasensis Guillén & Vargas, **sp. nov**., an endemic species from the northern region of Costa Rica, is described, photographed, and compared with the closest species, *V. aurantiaca*. The most notable differences are in the ovary, style, seeds, and especially the stigma. *Voyria aurantiaca* is distributed from Guyana, Brazil, Panama, Trinidad, Venezuela, and the Pacific side of Colombia to northern Ecuador.

RESUMEN

Voyria crucitasensis Guillén & Vargas, **sp. nov** , una especie endémica de la región norte de Costa Rica, se describe, fotografía, y compara con la especie más cercana, *V. aurantiaca*. Las diferencias más notables se ubican en el ovario, el estilo, las semillas y principalmente el estigma. *Voyria aurantiaca* se distribuye desde Guyana, Brasil, Panamá, Trinidad, Venezuela, y el costado Pacifico de Colombia hasta el norte de Ecuador.

La familia Gentianaceae Juss. posee una distribución cosmopolita, con casi 86 géneros y 1651 especies, en Costa Rica representada por 16 géneros y 31 especies (Sanchez 2010). El género *Voyria* Aubl. se distribuye en su mayoría en los Trópicos Americanos con 19 especies y una solo especies en el Oeste de África Tropical (Maas & Ruyters 1986). Costa Rica posee 8 especies incluyendo la aquí descrita, se distribuyen en los bosques húmedos, muy húmedos y pluviales, creciendo entre los 0–1700 msnm. Estas plantas se caracterizan por ser micoheterotróficas, sin clorofila, las hojas opuestas, reducidas y escamiformes. Se pueden confundir con otras micoheterotróficas de la familia Burmanniaceae Blume, aunque difieren, pues, estas presentan hojas alternas, flores 3 ó 6 meras y ovario ínfero (Maas & Maas-van de Kamer 2010).

Voyria crucitasensis Y. Guillén & G. Vargas, **sp. nov**. **TIPO: Costa Rica. Alajuela**. Terrenos de la empresa Industrias Infinito S.A., Crucitas de Cutris, 10° 51' 54" N, 84° 20' 40" W, 52 m elevación, 20 Jun 2012 (fr, fl), *Y. Guillén 16* (holotipo, **CR**; isotipos: **USJ**). Figuras 1-3.

Voyria crucitasensis is closely related to *V. aurantiaca*, differing from it in longer pedicels, shorter corollas, stamens inserted 1 mm below the throat, ovary fusiform without glandular marks, style shorter, stigma capitate with 4-5 lobes and minutely papillate, and globular thickenings inside the periclinal cells forming irregularly inrolled protrusions, without granular or verrucose bodies.

Hierba hasta 20 cm; *raíces* con forma de coral; *tallos* simples o raramente ramificados, acanalados, salmón-anaranjados, los entrenudos 1.5–3 cm. *Hojas* 3–5 x 1.5–3 mm, triangulares, salmón a salmón pálido, connatas basalmente, patentes, aquilladas, ápice acuminado. *Inflorescencia*

en dicasios con hasta 8 flores o reducidas hasta 1 ó 2 flores; brácteas y bractéolas similares a las hojas pero ligeramente más pequeñas, agudas; pedicelos 8–9 mm. *Flores* 5-meras; cáliz 6–8 mm, salmón, tubular, el tubo 3–4 mm, los lóbulos 3–4 x 1–1.5 mm, lineares, acuminados a agudos, aquillados; corola 1 cm, hipocraterimorfa, amarilla, el tubo 13.5–14 mm, amarillo claro, glabro pero después de la inserción de los estambres conspicuamente peloso, los lóbulos 4–5 x 2–3 mm, amarillos, oblongos, ápice corto acuminado, con indumento simple; estambres insertos a c. 1 mm por debajo de la garganta, los filamentos hasta 1 mm, glabros, las anteras 0.7–1 mm, dorsifijas, coherentes con el estigma, las tecas atenuándose hacia la base mucronulada; *ovario* 4.5 x 1.5 mm, fusiforme, anaranjado, sésil, sin marcas glandulares en la base, estilo 6–7 mm, anaranjado, más largo que el ovario, *estigma* capitado, amarillo, diminutamente papilado, provisto de 4–5 lóbulos ubicados lateralmente de menos de 1 mm. *Cápsula* 8.5 x 4 mm, fusiforme, medialmente dehiscente por medio de 2 valvas, unido por el estilo y manteniéndose el estigma, septicida; *semillas* más largas que anchas, sacciformes, con un hilo terminal acuminado; 245–330 um de largo, 100–150 um de ancho, radio 1.7 largo por ancho. Engrosamientos globulares en el interior de las células periclinales que forman protuberancias irregularmente enrolladas, sin cuerpos granulares o verrucosos. Límites anticlinales claros y delgados.

Especímenes adicionales examinados. **COSTA RICA. Alajuela.** Terrenos de Don Alfredo Arias, Crucitas de Cutris, 10° 51' 57" N, 84° 20' 43" W, 50 m elevación, 5 Ene 2013 (fr, fl), *Guillén, Montoya, y Cascante 27* (**CR**); Terrenos de Don Alfredo Arias, Crucitas de Cutris, 10° 53' 47" N, 84° 20' 25" W, 48 m elevación, 6 Ene 2013 (fr, fl), *Guillén, Cascante, y Montoya 28* (**CR**).

Distribución. Hasta ahora endémica de Costa Rica; se ha colectado en el bosque muy húmedo tropical de tierras bajas a 52 m de elevación en la zona norte de la vertiente del Caribe (Crucitas de Cutris, Alajuela).

Hábitat. Se colectó *Voyria crucitasensis* en un bosque maduro de al menos 40 años, suelo con suficiente materia en descomposición, 5 grados de pendiente, con un dosel aproximadamente de 20 m, bajo la sombra de árboles de *Meliosma sp.*, *Borojoa panamensis*, *Pentaclethra macroloba*, *Stryphnodendron macrostachyum*, *Croton smithianus*, *Pouroma bicolor, Colubrina spinosa,* y *Zanthoxylum sp.* *Voyria crucitasensis* también crece simpátricamente con *V. tenella.* Se han observado poblaciones de aproximadamente 20 individuos.

Fenología. Se ha recolectado con flores y frutos en Enero, Febrero, Junio, y Julio.

Etimología. El epíteto "crucitasensis" hace alusión al lugar de su colecta.

Voyria crucitasensis se puede reconocer en Costa Rica por presentar hojas de 3–5 x 1.5–3 mm; inflorescencia en dicasio con hasta 8 flores o reducidas hasta 1 ó 2 flores; pedicelos 8–9 mm; tubo del cáliz 3–4 mm; corola hasta 1 cm; lóbulos de la corola 4–5 x 2–3 mm; estambres insertos casi 1 mm por debajo de la garganta; ovario sin marcas glandulares; estilo 6–7 mm; estigma capitado, 4–5 lóbulos laterales, diminutamente papilado; cápsula medialmente dehiscente por 2 valvas; semillas con engrosamientos globulares en el interior de las células periclinales que forman protuberancias irregularmente enrolladas. Estas características no concuerdan con ninguna especie presente en el país por lo que se investiga con las otras especies publicadas del género, se puede comparar con *Voyria aurantica* que está presente desde Panamá hasta América del Sur. En la Flora Mesoamericana (Wilbur 2009), se reporta una colecta en Costa Rica de esta especie (*Kernan & Phillips 912* (MO)), posteriormente, en 1991 se determina que es *Voyria kupperi* (Suess.) Ruyters & Maas (TROPICOS 2014). La comparación entre *V. aurantiaca* y *V. crucitasensis* se da a razón de que ambas presentan el mismo tipo de raíz en coral, tallos anaranjados a salmonados, brácteas y bractéolas similares a las hojas, flores amarillas, pero *Voyria crucitasensis* se puede diferenciar por presentar hojas más pequeñas (3–5 x 1.5–3 mm vs. 3–10 x 1–4 mm), pedicelos más largos (8–9 mm vs. 3–7 mm), tubo

Figura 1. *Voyna crucitasensis* Y. Guillén & G. Vargas, hábito. Foto por Y. Guillén

Figura 2. *Voyria crucitasensis* Y. Guillén & G. Vargas. (sup.) Inflorescencia. (inf.) Detalle de los lóbulos de la corola. Fotos por Y. Guillén.

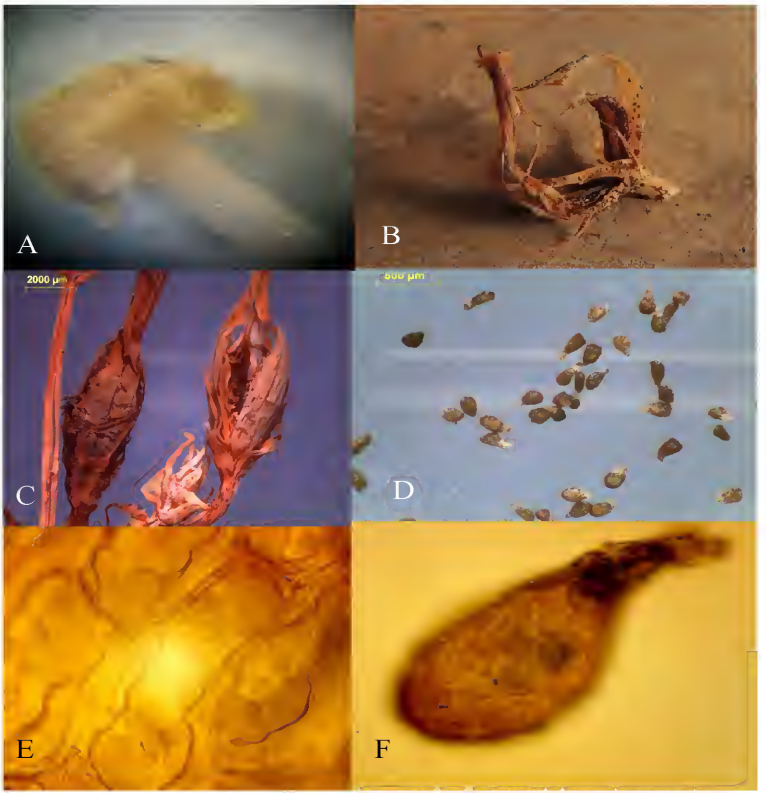

Figura 3. A-F. *Voyria crucitasensis* Y. Guillén & G. Vargas. A. Detalle de los lóbulos en el estigma y lo diminutamente papilado. B -C. Detalle del fruto. D. Semillas (50x). E. Detalle de las células en la superficie de la semilla (1000x). F. Detalle de la semilla (400x). Fotos por Y. Guillén (A-B) y G. Vargas (C-F)

del cáliz más largo (3–4 mm vs. 2–3 mm), corola más corta (1 cm vs. 1.5–3 cm), lóbulos de la corola más pequeños (4–5 x 2–3 mm vs. 2–10 x 1–3 mm), los estambres insertos a 1 mm (vs. 2–3 mm) por debajo de la garganta, el ovario fusiforme sin marcas glandulares (vs. angostamente oblongo-elíptico con marcas glandulares visibles), el estilo más corto (6–7 mm vs. 7–15 mm), estigma diminutamente papilado (vs. puberulento), semillas con engrosamientos globulares en el interior de las células periclinales que forman protuberancias irregularmente enrolladas, sin cuerpos granulares o

verrucosos (vs. engrosamientos en hileras, estos engrosamientos se unen para formar grumos compuestos, con cuerpos verrucosos en el exterior de la pared).

AGRADECIMIENTOS

A Luis Poveda (Universidad Nacional de Costa Rica) y Joaquín Sánchez (Museo Nacional de Costa Rica) por su colaboración en los inicios de la investigación. A Mike Grayum y Barry Hammel (Missouri Botanical Garden) por sus valiosos aportes y sugerencias; también a Mario Campos (Universidad Nacional de Costa Rica) y Alfredo Cascante (Universidad de Costa Rica) por la ayuda brindada. El primer autor quiere agradecer a Quírico Jiménez (Universidad Técnica Nacional) por su apoyo en el transcurso de la investigación.

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JOHN TORREY: A BOTANICAL BIOGRAPHY

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ABSTRACT

The role played by the American botanist John Torrey (1796–1873) in the development of floristics and the naming of plants, especially from the American West, is shown to be fundamental not only for present-day taxonomists in their monographic and floristics studies, and to historians in understanding the significance of discovering new and curious objects of nature in the exploration of the West but also the role Torrey directly and indirectly played in the development of such institutions as the New York Botanical Garden and the Smithsonian Institution. For the author of this 2014 paper, the name of John Torrey dates back to his earliest years of interests in botany, some 56 years ago, as even then Torrey was the kind of hero he could admire without resorting to comic books or movies.

John Torrey has long been a "founding father" of North American systematic botany. Even so it was probably a bit unusual that a high school kid from the Sierra Nevada of California should know the name and even something about the man. It was Torrey who described plants with the explorer John Charles Frémont[1], and so by fate the three of us were thrown together while I penned a paper for a history class at Sonora Union High School in the spring of 1958. Frémont brought a small howitzer with him on his third expedition to the West, and the weapon was buried in the Sweetwater Mountains of eastern California. It was what became of that howitzer, and the story around it, that was the focus of that term paper, except that Frémont had a propensity to talk about plants and geology, and so attention was drawn to an appendix — "Descriptions of some new genera and species of plants"[2] — and by extension to John Torrey.

Here was a description and image of *Pinus monophylla*, the singleleaf pinyon so common in the Great Basin. Exploring another Torrey paper, "Plantae Frémontianae," published in 1853 by the Smithsonian Institution, here again were wonderful descriptions and Isaac Sprague's[3] illustrations of plants common around my boyhood home of Pinecrest in Tuolumne County: *Spraguea umbellata* (pussypaws, now *Cistanthe umbellata*), *Libocedrus decurrens* (incense cedar, now *Calocedrus decurrens*), *Chamaebatia foliolosa* (mountain misery), and most significantly, *Sarcodes sanguinea* (locally known as "snowplant," Fig. 1)[4]. There were others illustrations, all elegantly executed, but the snowplant — well, who could not experience the same amazement Frémont must have felt when he first encounter this plant! Torrey was more refined: "A very interesting plant," he wrote, "belonging to the small group of Monotropeae." How could he have been so calm given its "fleshy texture and blood-red color." What followed were the words of a professional botanist, a full and detailed description followed by a technical discussion. Interesting and most curious to a high school junior!

Decades later, working from conjectures in a 1985 paper in a botanical journal[5] (my high school history paper still finding life!), the Forest Service, and now others, found pieces of the carriage that transported the howitzer.

As for Torrey, Frémont, and the plants, a great deal more was learned over those same decades. Today, in the LuEsther T. Mertz Library at the New York Botanical Garden, one can put all of the pieces together, for here one can see the original Charles Sprague drawings, proofs of the

illustrations, and the final published results, and from the William and Lynda Steere Herbarium one can see the original Frémont specimens, all carefully preserved. And as one learns more about when and how the Frémont collections were made — carried across the continent horseback in bundles wrapped in canvas and hides, moved by steamboat and carriage to Washington and finally to New York — one discovers incredible stories that only explorers and botanists and specimens can tell.

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Figure 1 *Sarcodes sanguinea* Torr — A digital painting by J L Reveal

Just look at collection no 367 *Pinus monophylla* (figs 2, 3) A single herbarium specimen with a marked over printed label "Fremont's Expedition to California 184[4 in ink] / 367 1844 / Pinus monophylla / Torr" So little written, so much said Turning to the 1845 Torrey and Fremont report (page 319) one reads "This tree, which is remarkable among the true pines for its solitary leaves, is extensively diffused over the mountains of Northern California, from long 111° to 120° and through a considerable range of latitude" It is alluded to repeatedly in the course of Fremont's narrative, as the "*nut pine*" From page 319 one goes to page 221 to read the events of January 24th 1844 to find the story behind the specimen

> A man was discovered running towards the camp as we were about to start this morning, who proved to be an Indian of rather advanced age — a sort of forlorn hope, who seemed to have been worked up into the resolution of visiting the strangers who were passing through the country He seized the hand of the first man he met as he came up, out of breath, and held on, to assure himself protection He brought with him in a little skin bag a few pounds of the seeds of a pine tree which to-day we saw for the first time, and which Dr Torrey has described as a new species, under the name of *pinus monophyllus*; in popular language, it might be called the *nut pine*. We purchased them all from him. The nut is oily of very agreeable flavor, and must be very nutritious, as it constitutes the principal subsistence of the tribes [the Kucadikadi, a group of northern Piute] among which we were now travelling

On that day Fremont and his men were in the pine-covered Masonic Mountains north of Bridgeport, and the howitzer remained with them for at least for five more days They were about to cross the Sierra Nevada in the dead of winter For me, a 114 years later, this was grand adventure!

Figure 2 *Pinus monophylla* Torr & Frem

Source BHL

Figure 3 Isaac Sprague illustration of *Pinus monophylla*

John Torrey's early years

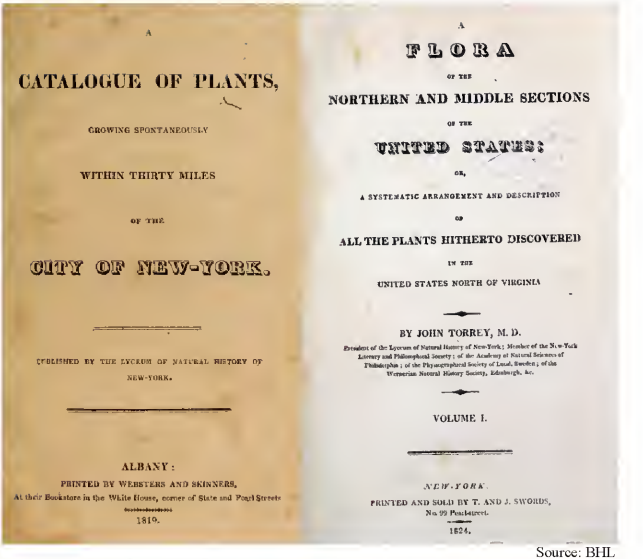
John Torrey was born on August 15, 1796, in New York City and came to botany as a secondary career[6]. He was for most of his professional career a chemist, serving in that capacity at the United States Military Academy at West Point (1824–1827), at New York College of Physicians and Surgeons (now Columbia University; 1827–1855), and at Princeton University (1830–1855). For the last twenty years of his life he was Assayer of the Mint in New York (1853–1873). He earned his medical degree at the College of Physicians and Surgeons in 1818 and briefly practiced (1818–1822) although this seems to have been rather secondary compared to his efforts with the newly established Lyceum of Natural History of New York, as he was among the institution's first curators, starting in 1817[7].

The role young Torrey played in the development of the Lyceum proved to be critical, because as a result of his broad interests, he and the other curators were able to assemble one of the most extensive collections of natural history objects then in America. At this time, Torrey's interest in botany focused mainly on cryptogams, especially on the fungi, mosses, and bryophytes. It was during this period, with the help of others, that he acquired a fine set of watercolors of fungi as well as many specimens. Even though Torrey longed for a good microscope, he worked on sedges (mainly the genus *Carex*) and looking today at his detailed sketches of those tiny flowers and fruits on herbarium sheets in Torrey's herbarium at the New York Botanical Garden, it is amazing what he was able to discern with his simple lenses and, no doubt, a lot of patience.

Torrey's interests in natural history, while catholic, were heavily weighted toward botany, having been influenced as a youngster by Amos Eaton[8], a noted amateur botanist and lawyer who was imprisoned in 1811 for forgery. Torrey's father, William, a sound businessman, city alderman, and fiscal agent to the state prisons, took John with him to Newgate Prison where young John became the conduit that moved plants from beyond the walls to Eaton within. At fourteen, this association had an impact for by the time Torrey became curator at the Lyceum, he was already engaged with others in writing *A Catalogue of Plants* (Fig. 4a) published in 1819[9]. In a series of notes at the end of the book, several new species were described by Torrey.

Torrey's annotated copy of the *Catalogue* is in the rare book room of the Mertz Library. There are some corrections, but more importantly are the additions. Not only are newly found plant mentioned in this interleafed copy, it is clear that Torrey was already expanding the reach of the *Catalogue*, writing in plants found over much of New York and even New England. Without doubt, Torrey's annotations formed the basis for his later *A Flora of the Northern and Middle Sections of the United States* (Fig. 4b), published in three parts from September of 1823 until July of 1824. This work was an immediate success and introduced Torrey to others interested in plants, especially those across the Atlantic. This was promptly followed by his *Compendium of the Flora of the Northern and Middle States* published in 1826 (Fig. 5).

One holds Torrey's copy *Compendium* with reverence. The cover is worn, the pages look like they have seen rain suggesting that this book was carried when John traveled. There are faint pencil corrections, additions, comments. The preface indicates that it was written at West Point. For a modern reader the book might be frustrating as it is arranged according to the Linnaean sexual system. Still, tucked off to the side of many generic names are the natural family names championed by French botanist Antoine Laurent de Jussieu — Atriplices, Borragineae, Caryophylleae, Passiflorae — a hint of things to come[10]. There were no keys for one simply knew that the *Diadelphia* and *Decandria* were the homes of the pea family. Typically there were brief descriptions of genera and each species was briefly characterized. Thus, by counting the stamens and the number of carpels, one could arrive at the proper spot in the book and then glance down the page for the unique diagnostic features that characterized the plant in hand.



A

CATALOGUE OF PLANTS,

GROWING SPONTANEOUSLY

WITHIN THIRTY MILES

OF THE

CITY OF NEW-YORK.

PUBLISHED BY THE LYCEUM OF NATURAL HISTORY OF NEW-YORK.

ALBANY:
PRINTED BY WEBSTERS AND SKINNERS,
At their Bookstore in the White House, corner of State and Pearl Streets
1819.

A

FLORA

OF THE

NORTHERN AND MIDDLE SECTIONS

OF THE

UNITED STATES:

OR,

A SYSTEMATIC ARRANGEMENT AND DESCRIPTION

OF

ALL THE PLANTS HITHERTO DISCOVERED

IN THE

UNITED STATES NORTH OF VIRGINIA

BY JOHN TORREY, M. D.

President of the Lyceum of Natural History of New-York; Member of the New-York Literary and Philosophical Society; of the Academy of Natural Sciences of Philadelphia; of the Physiographical Society of Lund, Sweden; of the Wernerian Natural History Society, Edinburgh, &c.

VOLUME I.

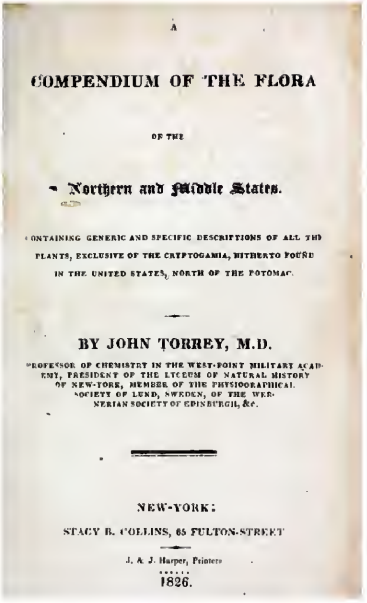
NEW-YORK:
PRINTED AND SOLD BY T. AND J. SWORDS,
No. 99 Pearl-street.
1824.

Source: BHL

Figure 4 (a) Title page of *Catalogue* (1819) and (b) the 1824 *Flora*.

His duties as curator meant that Torrey's interests were destined to go beyond the cryptogam world. Long before Frémont, Torrey was involved in examining vascular plants gathered by western expeditions. In an 1823 paper in the *Annals of the Lyceum of Natural History of New York*, Torrey wrote "Descriptions of some new or rare plants from the Rocky Mountains, collected in July, 1820, by Dr. Edwin James"[11]. Here one finds many of the novel plants found on what is now unfortunately called Pikes Peak rather than the much more suitable James Peak as it was then known[12].

In a series of articles published from December of 1826 until June of 1827, Torrey augmented that paper with a much longer and more detailed account in the *Annals*, discussing some 481 different plants. Over that five-year period Torrey's knowledge of plants grew tremendously. While James himself named some of his new finds, notably the limber pine (*Pinus flexilis*), a bluebell (*Mertensia ciliata*; Fig. 6) and the columbine (*Aquilegia coerulea*; Fig. 34) in late December of 1822, it remained for Torrey to deal with the bulk of new species, notably *Krameria lanceolata* (trailing krameria) of the Great Plains, *Acer glabrum* (Rocky Mountain maple) of the lower elevations in the Rockies, and *Prosopis glandulosa* (honey mesquite), a major desert shrub of the Southwest illustrated by Torrey himself[13].



A

COMPENDIUM OF THE FLORA

OF THE

Northern and Middle States.

CONTAINING GENERIC AND SPECIFIC DESCRIPTIONS OF ALL THE PLANTS, EXCLUSIVE OF THE CRYPTOGAMIA, HITHERTO FOUND IN THE UNITED STATES, NORTH OF THE POTOMAC.

BY JOHN TORREY, M.D.

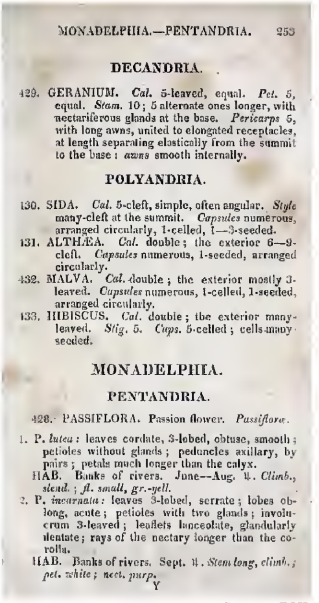
PROFESSOR OF CHEMISTRY IN THE WEST-POINT MILITARY ACADEMY, PRESIDENT OF THE LYCEUM OF NATURAL HISTORY OF NEW-YORK, MEMBER OF THE PHYSIOGRAPHICAL SOCIETY OF LUND, SWEDEN, OF THE WERNERIAN SOCIETY OF EDINBURGH, &c.

NEW-YORK:

STACY B. COLLINS, 65 FULTON-STREET

J. & J. Harper, Printers

1826.



MONADELPHIA.—PENTANDRIA. 253

DECANDRIA.

429. GERANIUM. *Cal.* 5-leaved, equal. *Pet.* 5, equal. *Stam.* 10; 5 alternate ones longer, with nectariferous glands at the base. *Pericarps* 5, with long awns, united to elongated receptacles, at length separating elastically from the summit to the base: *awns* smooth internally.

POLYANDRIA.

430. SIDA. *Cal.* 5-cleft, simple, often angular. *Style* many-cleft at the summit. *Capsules* numerous, arranged circularly, 1-celled, 1—3-seeded.
431. ALTHÆA. *Cal.* double; the exterior 6—9-cleft. *Capsules* numerous, 1-seeded, arranged circularly.
432. MALVA. *Cal.* double; the exterior mostly 3-leaved. *Capsules* numerous, 1-celled, 1-seeded, arranged circularly.
433. HIBISCUS. *Cal.* double; the exterior many-leaved. *Stig.* 5. *Caps.* 5-celled; cells many-seeded.

MONADELPHIA.

PENTANDRIA.

426. PASSIFLORA. Passion flower. *Passiflora.*

1. P. *lutea*: leaves cordate, 3-lobed, obtuse, smooth; petioles without glands; peduncles axillary, by pairs; petals much longer than the calyx.
HAB. Banks of rivers. June—Aug. ♃. *Climb., stand.; fl. small, gr.-yell.*
2. P. *incarnata*: leaves 3-lobed, serrate; lobes oblong, acute; petioles with two glands; involucrum 3-leaved; leaflets lanceolate, glandularly dentate; rays of the nectary longer than the corolla.
HAB. Banks of rivers. Sept. ♃. *Stem long, climb.; pet. white; nect. purp.*

Y

Source: BHL

Figure. 5. Title page and a representative page of the *Compendium.*

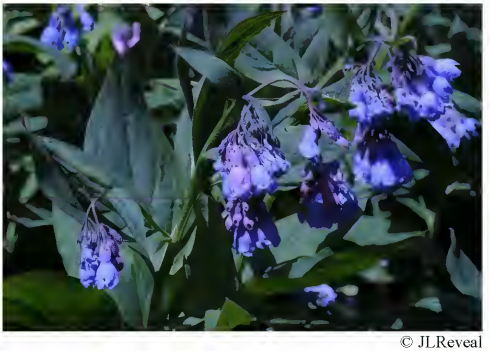


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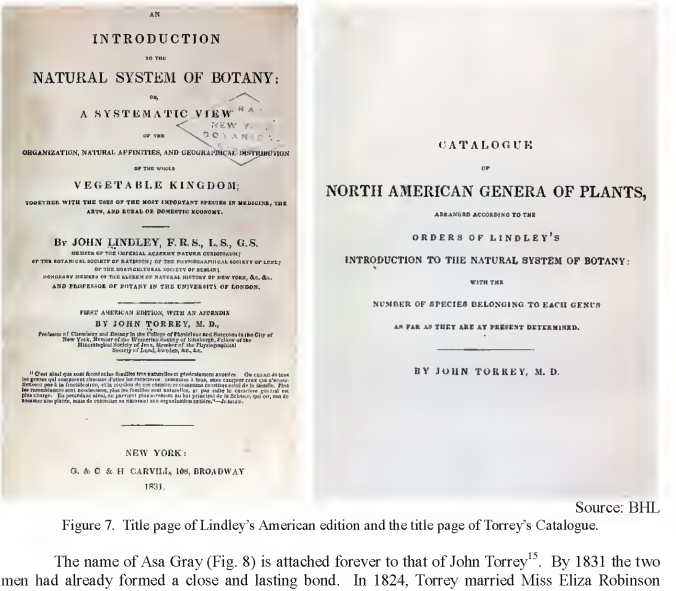
Figure 6. *Mertensia ciliata* (James ex Torr.) G. Don

Torrey's paper on the James collection departed from the Linnaean system and embraced that of Jussieu's being the first author in North America to adopt natural families. Soon thereafter, in 1830[14], England's John Lindley published a new botany text book on the natural system, and immediately Torrey asked Lindley's permission to publish an American edition (Fig. 7). In the 1831 American edition, Torrey added a "Catalogue of North American genera of plants." To ensure the wide dissemination of the natural system, Torrey reprinted his *Catalogue* with its own pagination. By 1831, Torrey listed his title as "Professor of Chemistry and Botany in the College of Physicians in the City of New York."



AN

INTRODUCTION

TO THE

NATURAL SYSTEM OF BOTANY;

OR,

A SYSTEMATIC VIEW

OF THE

ORGANIZATION, NATURAL AFFINITIES, AND GEOGRAPHICAL DISTRIBUTION

OF THE WHOLE

VEGETABLE KINGDOM;

TOGETHER WITH THE USES OF THE MOST IMPORTANT SPECIES IN MEDICINE, THE ARTS, AND RURAL OR DOMESTIC ECONOMY.

By JOHN LINDLEY, F.R.S., L.S., G.S.

MEMBER OF THE IMPERIAL ACADEMY NATURÆ CURIOSORUM;
OF THE BOTANICAL SOCIETY OF RATISBON; OF THE PHYTOGRAPHICAL SOCIETY OF LONDON;
OF THE HORTICULTURAL SOCIETY OF BERLIN;
HONORARY MEMBER OF THE LYCEUM OF NATURAL HISTORY OF NEW YORK, &c. &c.
AND PROFESSOR OF BOTANY IN THE UNIVERSITY OF LONDON.

FIRST AMERICAN EDITION, WITH AN APPENDIX
BY JOHN TORREY, M. D.,
Professor of Chemistry and Botany in the College of Physicians and Surgeons in the City of New York, Member of the Wernerian Society of Edinburgh, Fellow of the Hitchcockian Society of Jena, Member of the Physiographical Society of Lund, Sweden, &c. &c.

"C'est ainsi que sont formées celles-feuilles très naturelles et généralement avouées. On essaie de tirer les genres qui composent chacune d'elles les caractères communs à tous, sans craindre assez que la plupart de ces caractères ne soient pas applicables à tous les genres, et que, par conséquent, ils ne puissent pas être remarquables aux botanistes, plus les familles sont naturelles, et plus cette ils observent qu'il est plus exact. En procédant ainsi, on parvient plus sûrement au but proposé de la Science; qui est, non de former des plants, mais de connaître et nommer les vrais rapprochements naturels."—DE CANDOLLE.

NEW YORK:

G. & C. & H. CARVILL, 108, BROADWAY

1831.

CATALOGUE

OF

NORTH AMERICAN GENERA OF PLANTS,

ARRANGED ACCORDING TO THE

ORDERS OF LINDLEY'S

INTRODUCTION TO THE NATURAL SYSTEM OF BOTANY:

WITH THE

NUMBER OF SPECIES BELONGING TO EACH GENUS

AS FAR AS THEY ARE AT PRESENT DETERMINED.

BY JOHN TORREY, M. D.

Source: BHL

Figure 7. Title page of Lindley's American edition and the title page of Torrey's Catalogue.

The name of Asa Gray (Fig. 8) is attached forever to that of John Torrey[15]. By 1831 the two men had already formed a close and lasting bond. In 1824, Torrey married Miss Eliza Robinson Shaw of New York City and the couple was living comfortably at West Point. Professionally, Torrey was deep into chemistry, with botany on the side. His long-time correspondent, Lewis David von Schweinitz[16], had finished a monograph of the genus *Carex* that Torrey carefully edited for the *Annals*, becoming in essence a co-author. By this time, Torrey and von Schweinitz were talking about authoring a cryptogam flora of the United States and the latter's trip to Europe was largely designed to obtain books, specimens, and familiarity with American species already named by European botanists. Unfortunately, there was a dispute with Chester Dewey[17], professor of natural history at Williams College, over who had the right to publish on *Carex*. The letters in the archives at the New York Botanical Garden tell the story, an invaluable resource to both historians and botanists, about early botanical struggles for scientific priority in the United States. Dewey published a few new

species just before von Schweinitz, much to Torrey's distress, and the letters show both groups were trying to claim ownership of the genus. Torrey and von Schweinitz danced around this problem for years, with Dewey publishing a name here and there as parts of his "Caricography" series. Whether or not one can be so kind as Asa Gray was in his 1873 obituary of Torrey[18] and say that "Torrey generously turned over the Carices to the late Professor Dewey" is a matter of debate, as Gray was not entirely an aloof bystander in this matter. In 1836 Torrey published his own "Monograph of North American Cyperaceae" with Rhynchosporeae revised "entirely" by Asa Gray whose own monograph of *Rhynchospora* was published at the same time in the *Annals*.

Ah, the letters are amazing!

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Figure 8. Asa Gray

John Torrey's first letter from Asa Gray arrived in September of 1830[19]. Working both at the College of Physicians and Surgeons in New York and at Princeton University in nearby New Jersey, Torrey's botanical efforts were stretched thin in an effort to survive the rigors of teaching and providing for his family. He needed help and Gray became a possible candidate.

Asa Gray received his medical degree in 1831 at the age of twenty, nearly a full year before he legally was able to practice. His early years were a jumble of semi-failed attempts at being a physician and teaching high school, mainly in Utica, New York. Frustrated by his efforts as a doctor, and ecstatic about botany, it was inevitable that Torrey's suggestion that the young man should become an expedition surgeon/naturalist meant that the two would meet. When Torrey decided to go to Europe, mainly in search of a decent microscope, he asked Gray to collect plants and to organize his personal herbarium. This Gray did in the summer of 1833. By the fall of 1834, Gray was living in Torrey's home, free at last to write botanical papers much to the dismay of his parents and their rapidly disappear dreams of a doctor-son.

Gray's duties were relatively simple: Help Torrey with his "botanical & chemical labours" and Gray was permitted to "devote part of his time to his own concerns"[20]. With Gray at hand, talk shifted from a cryptogam flora to simply a flora of the United States, and even that would morph into the ultimate title, *A Flora of North America.*

The idea of a flora was discussed by Torrey with William Jackson Hooker[21] (Fig. 9) in Scotland, who was then engaged in publishing *Flora Boreali-Americana* — basically a flora of that portion of North America controlled by Great Britain. Not only did Torrey obtain parts of the *Flora* already published but also critical specimens as well, especially those found by David Douglas (Fig. 9) in the Oregon Country[22]. In Paris, Torrey was able to obtain a copy of André Michaux's 1803 *Flora Boreali-Americana*[23] and again a promise of specimens. On his three-month visit Torrey met the likes of George Bentham[24] (Fig. 10), Robert Brown[25], John Lindley (Fig. 10), and a host of others. Most importantly, Torrey studied Michaux's American collections, clearly with the goal of writing a flora of the North America.

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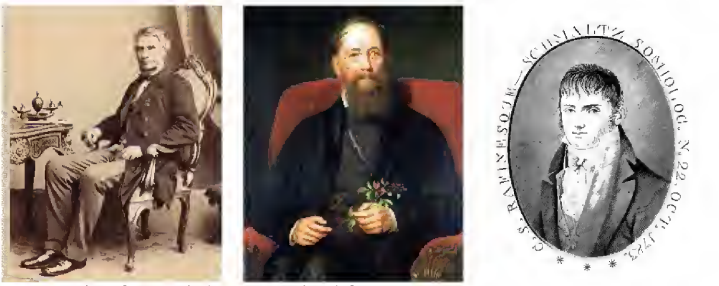
Figure 9. William Jackson Hooker (left) and David Douglas (right).



© Hunt Institute for Botanical Documentation (left)

Figure 10. George Bentham (left), John Lindley, Constantine Samuel Rafinesque (right).

Looking at the books Torrey gathered in Europe in the Mertz Library one finds a treasure trove of comments, notes, and thoughts. By studying the marginalia one can see the formation of ideas that would find their way into his *Flora*. Knowledge of Torrey's proposed flora meant that individual collectors began to send him more and more specimens, their curation and arrangement into the herbarium being left largely to Gray. Two long-time friends, Constantine Samuel Rafinesque[29] (Fig. 10) and Charles Wilkins Short[30], continued with their contributions to Torrey and now plants also came from the South, sent by a multitude of new collectors — Moses Ashley Curtis[26], Hardy Bryan Croom[27], and John Leonard Riddell[28] (Fig. 11) to mention only a few.

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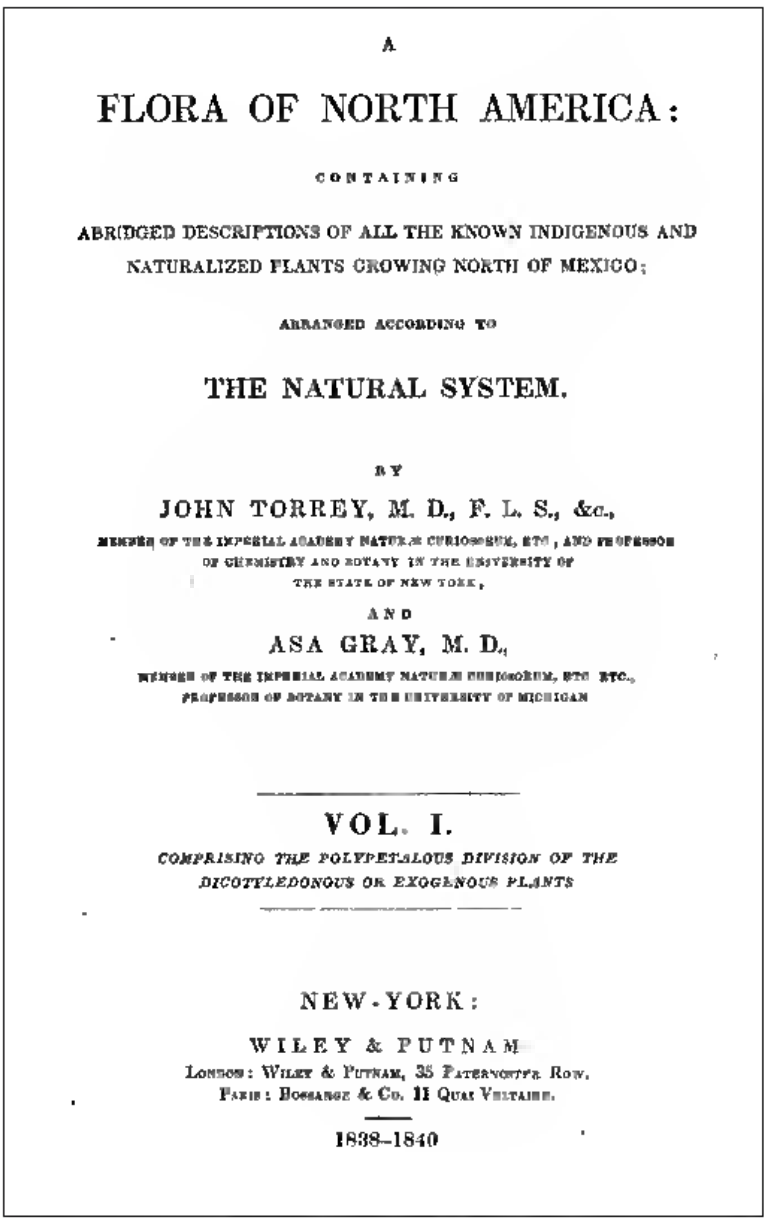
Figure 11. Moses Ashley Curtis (left), John Leonard Riddell, Hardy Bryan Croom (right).

Rafinesque and Torrey knew each other from the early days of the Lyceum. Rafinesque even tried to get Torrey to join him at the University of Transylvania in 1819. By the 1830s, with the prolific Rafinesque busily publishing hundreds of new scientific names, much to the dismay of Torrey, their association was at an end professionally. Even so, Torrey's letter to and from Rafinesque are filled with pleasant exchanges, suggesting that while they might differ as botanists, they were still friends. Short, always a major collector, continued to be so for decades. The letters between Torrey and Short are diverse and filled with both scientific and personal matters. Above all, as their

correspondence matured and both men aged, their interest and frustrations revolved around Torrey's *Flora* (Fig 12)



A

FLORA OF NORTH AMERICA:

CONTAINING

ABRIDGED DESCRIPTIONS OF ALL THE KNOWN INDIGENOUS AND NATURALIZED PLANTS GROWING NORTH OF MEXICO;

ARRANGED ACCORDING TO

THE NATURAL SYSTEM.

BY

JOHN TORREY, M. D., F. L. S., &c.,

MEMBER OF THE IMPERIAL ACADEMY NATURÆ CURIOSORUM, ETC., AND PROFESSOR OF CHEMISTRY AND BOTANY IN THE UNIVERSITY OF THE STATE OF NEW YORK,

AND

ASA GRAY, M. D.,

MEMBER OF THE IMPERIAL ACADEMY NATURÆ CURIOSORUM, ETC. ETC., PROFESSOR OF BOTANY IN THE UNIVERSITY OF MICHIGAN

VOL. I.

COMPRISING THE POLYPETALOUS DIVISION OF THE DICOTYLEDONOUS OR EXOGENOUS PLANTS

NEW-YORK:

WILEY & PUTNAM

LONDON: WILEY & PUTNAM, 35 PATERNOSTER ROW.

PARIS: BOSSANGE & Co. 11 QUAI VOLTAIRE.

1838–1840

Source BHL

Figure 12 Title page of Torrey and Gray's *Flora of North America*

The basic question was always how best could the *Flora* be done efficiently, given the constant flow of new material from the South and West. The keys, plain and simple, were Asa Gray and Thomas Nuttall.

With Asa Gray firmly with Torrey in New York, even though Gray would be offered a professorship with the not-yet-established University of Michigan in 1838, he was basically living with Torrey (or living in Torrey's house when the family was in Princeton) and writing treatments for what was now Torrey and Gray's *Flora*. Letters flowed between the two men that give some idea as to what was being accomplished, but there is little in the way of the intimate detail on how taxonomic decisions were reached or who was writing what. Based on what one can surmise from the letters at the New York Botanical Garden and at the Gray Herbarium at Harvard University, it would appear that Gray was the writer, with Torrey the editor and final arbiter on all matters in most taxonomic groups. Still, Gray carved out distinct areas of his own — most notably the sunflower family, Asteraceae — which Torrey gladly abandoned to the younger man.

One reason for the segregation of effort was that Torrey's role in botany was being expanded by other events. In 1835, the New York General Assembly directed the Secretary of the State to report on the natural history and geology of the state. On the first of July in 1836, Torrey began to compile a flora of New York. This single task would take five years and the first volume (Fig. 14) was not published until January of 1843, a few days before the last part of Torrey and Gray's *Flora* was published in February of that year.

The pivotal person in all of this was Thomas Nuttall[31] (Fig. 13). English by origin, Nuttall first came to the United States in 1808 and collected in the Old Northwest in 1810 for Benjamin Smith Barton (1766–1815) of Philadelphia. In 1811, Nuttall ventured up the Missouri River collecting plants from St. Louis to Fort Mandan. The threat of war, which began in 1812, caused Nuttall to return to England in late 1811, where he stayed until 1815. Back in Philadelphia, Nuttall published *The Genera of North American Plants* in 1818 (Fig. 14), setting himself up as a major taxonomist in America. He continued to explore in the South and along the Red River on the southern border of the Louisiana Territory. In 1823, Nuttall went to Harvard and remained there for the next eleven years. The desire to travel westward final got to him and Nuttall left Harvard in 1834[32] and went to Oregon and California, returning to Philadelphia in 1836 with thousands of specimens representing hundreds of new species (Figs. 15–16). No flora of North America could be accomplished without access to Nuttall's specimens. Torrey was unwilling to offer Nuttall an authorship, but was eager to publish his new species. Thus, from June of 1838, when the first part of the *Flora* was published, until February of 1843, when the last part was presented to the public, new species named or found by Thomas Nuttall were routinely proposed in Torrey and Gray's *Flora*.

That the *Flora* was never finished can be laid, in one sense, at the feet of Thomas Nuttall. Nuttall's departure from Harvard left a vacancy and it was destined to be filled by Asa Gray. Torrey was firmly established in New York and Princeton, and Gray had a position, of sorts, with the University of Michigan. In 1842, giving up on Michigan, Gray secured the position at Harvard with the charge of giving lectures in botany and being superintendent of the botanic garden. This move meant that Torrey's writing arm, which had allowed him to teach, was gone, leaving him alone at the very moment western North American explorations were fundamentally changing systematic botany in North America by virtue of a wealth of discoveries of new genera and species. That Gray's move to Harvard ultimately would be a plus to Torrey, and especially to the future of systematic botany, floristics, and biogeography, was not something that could remotely be construed as an immediate comfort to Torrey as he witnessed the multitude of specimens crossing his desk.

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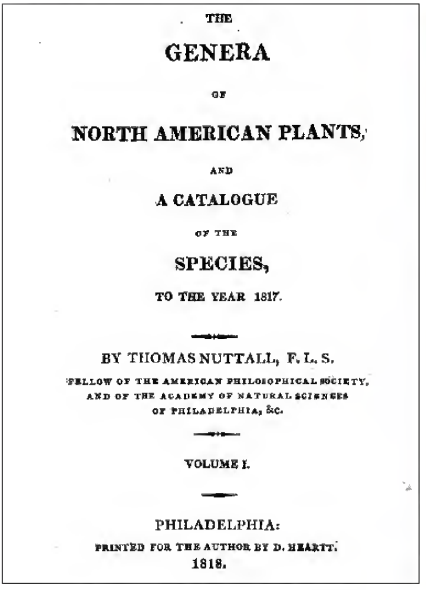
Figure 13. Thomas Nuttall and *Iris missouriensis* Nutt.



THE

GENERA

OF

NORTH AMERICAN PLANTS,

AND

A CATALOGUE

OF THE

SPECIES,

TO THE YEAR 1817.

BY THOMAS NUTTALL, F. L. S.

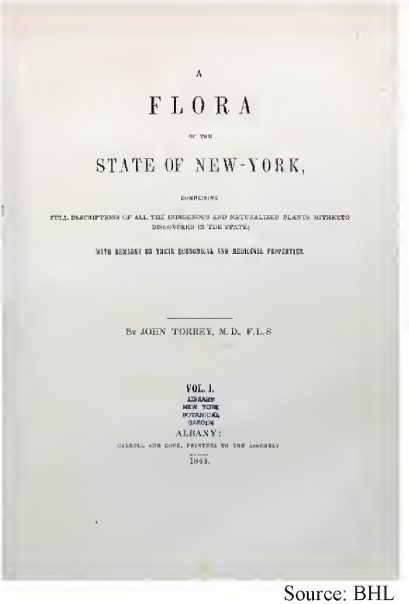
FELLOW OF THE AMERICAN PHILOSOPHICAL SOCIETY,
AND OF THE ACADEMY OF NATURAL SCIENCES
OF PHILADELPHIA, &C.

VOLUME I.

PHILADELPHIA:

PRINTED FOR THE AUTHOR BY D. HEARTT.

1818.



A

FLORA

OF THE

STATE OF NEW-YORK,

COMPRISING

FULL DESCRIPTIONS OF ALL THE INDIGENOUS AND NATURALIZED PLANTS HITHERTO
DISCOVERED IN THE STATE;

WITH REMARKS ON THEIR ECONOMICAL AND MEDICINAL PROPERTIES.

By JOHN TORREY, M.D. F.L.S.

VOL. I.

ALBANY:

1843.

Source: BHL

Figure 14. Title page of Nuttall's *Genera* and the title page of Torrey's *Flora.*

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Figure 15. *Clematis ligusticifolia* Nutt

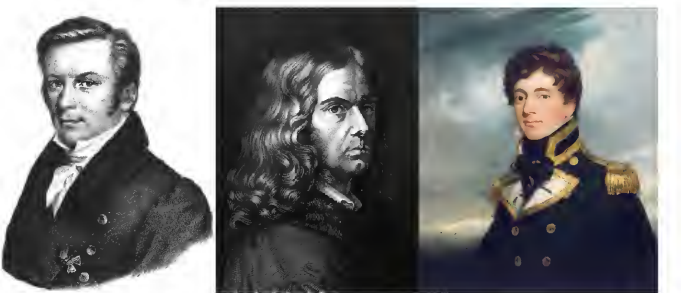
© JLReveal

Figure 16. *Stephanomeria exigua* Nutt

Torrey's labors on *A Flora of the State of New York*, published in 1843 in two volumes of more than a thousand pages and some 160 lithograph plates, was well received and laid a firm foundation for the continuation of *Flora of North America*. There were plans and hopes to do more, but first Gray had to get settled into his new position at Harvard, and Torrey — ever in the classroom — was doing his best to keep up with his botanical duties. He liked Lindley's 1835 *Ladies' Botany*, but instead of having this book published in America he issued his own version as lithographed class notes under the title of *Outlines of Botany* in 1841. Few copies of this work exist, and interestingly the copy at the Mertz Library lacks a date, suggesting that copies were likely printed as needed by students. Gray, too, was in the textbook business, dominated then by Amos Eaton and Almira Hart Lincoln (later Phelps). Her books, *Familiar Lectures on Botany* (1829) and *Botany for Beginners* (1833a), were widely used in girls' schools and academies, while Eaton's *Botanical Exercises* (1820) was designed for the male side. Gray's addition, initially titled *Elements of Botany* (1836) and then *The Botanical Text-book for College, Schools and Private Students* (1842), quickly became the new standard and like those of Eaton and Lincoln, Gray's own *Botanical Text-book* would undergo numerous revisions and printings[33].

John Torrey's role in westward expansion and botanical explorations

Although Thomas Jefferson had championed the notion of western explorations across the American continent, interest in government expeditions waned and the opening of the West was left to entrepreneurs, especially those engaged in the fur trade[34]. Along the Pacific Coast, sea-borne naturalists visited various ports of call, namely Johann Friedrich Gustav von Eschscholtz (1793–1831, Fig. 17 — left) and Ludolf Adelbert von Chamisso (1761–1838; Fig. 17 — center) aboard the Russian vessel *Rurik* (1816), Alexander Collie (1793–1835) and George Tradescant Lay (1799–1845) aboard the British vessels *Blossom* on Captain Frederick William Beechey's (1796–1856 — Fig. 17, right; Fig. 18) voyage (1826–1827), Paola Emilia Botta (1802–1870) aboard the French vessel *Héros* (1827–1828), and Richard Brinsley Hinds (1812–1846) on *H.M.S. Sulphur* (1837, 1839), as well as naturalists supported by the Hudson's Bay Company in the Pacific Northwest, such as David Douglas, John Scouler (1804–1871), William Fraser Tomie (1812–1886), Meredith Gairdner (?–1840), and John McLeod (1795–?). Mexico dominated California and much of the Southwest, and while a few individuals, such as Thomas Coulter (1793–1843) crossed the deserts of the Southwest in 1832 to join up with Douglas in California (Coville 1895; Nelson 1988), only a few plants were actually from the deserts of the West[35].



↑ © National Maritime Museum

Figure 17. J.F.G von Eschscholtz L.A. von Chamisso F.W. Beechey

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Figure 18. *Grindelia hirsutula* Hook. & Arn.

For Torrey, essentially everything went to European botanists and, at best, all he received were already named specimens. The desire to get American naturalists into the field, especially in the West, was therefore of critical importance to him especially if a flora of North America was to be written.

"Manifest Destiny" was a political catch phrase championed by Senator Thomas Hart Benton of Missouri[36], the father of Jessie Benton Frémont. Who better to lead the westward expansion of the United States than his own son-in-law whom Benton could influence? Frémont's success as a writer, due in large part of the editorial pen of Jessie, was a surprise for Frémont's report was an exciting read that caused many to consider moving to the West. Frémont's third expedition left St. Louis on the first of June in 1845 with Kit Carson[37] and a number of other "mountain men" in his party of 55. His military orders were to explore the east side of the Rocky Mountains to the source of the Arkansas River. His "Manifest Destiny" orders were to go immediately to California as war with Mexico was possible, and the champion of "Destiny" wanted an American present to be there in case California could be captured for the United States. In this way Frémont was in California for the Bear Flag Revolt[38], the conquest of California accomplished with his small band, a contingent of naval personnel lead by Commodore Robert F. Stockton[39] and several Americans already in resident. This resulted in Frémont's appointment by Stockton as the military governor of California. Frémont's refusal to step down from this appointment when Brigadier General Stephen Watts Kearney[40] ordered Lieutenant Colonel Frémont to do so resulted in Fremont's arrest and court-martial. Convicted but pardoned immediately by President James K. Polk, Frémont resigned his commission and moved to California, where he settled, albeit only on paper, on his Spanish land grant Rancho las Mariposas in

the foothills of the Sierra Nevada near the entrance to Yosemite Valley in the middle of what, two years later, would be the Mother Lode of California's gold country.

In spite of all these military matters, Frémont gather plants which soon found their way to John Torrey and formed the basis of his "Plantae Frémontianae" published in 1853 in the *Smithsonian Contributions to Knowledge*, where Torrey proposed such new genera as *Sarcodes*, *Carpenteria*, *Sprague*a, *Coleogyne*, and *Emplectocladus* (Fig. 19). Among his new species was *Calocedrus decurrens* (Torr.) Florin (Fig. 20) and a full description and an image of *Chamaebatia foliolosa* Benth. (Fig. 21)[41].

The botanical novelties gathered on the Wilkes Expedition[42], a round-the-world voyage that lasted from 1838 to 1842, fell to Gray with Torrey dealing only with the small collections made in the Pacific Northwest. As a result Torrey published another new genus in the *Contributions*, the magnificent *Darlingtonia californica* (Fig. 22), elegantly illustrated by Isaac Sprague.

Torrey's reports on the early western expeditions were crisply written and detailed only enough to be useful to fellow botanists. It seems that Torrey was not particularly interest in the plants of areas already explored botanical so that his 1843 summary of the collections made by Charles Geyer[43] in the region between the Mississippi and Missouri rivers was almost pedestrian[44]. Besides, Torrey was more engaged in writing and then publishing, in 1853, his *Botany of New-York*, a revision of his 1841 and 1843 summaries, to which annual supplements subsequently would be added by George William Clinton (1807–1885) of Buffalo and by Charles H. Peck (1833–1913) of Albany from 1865 to 1915[45].

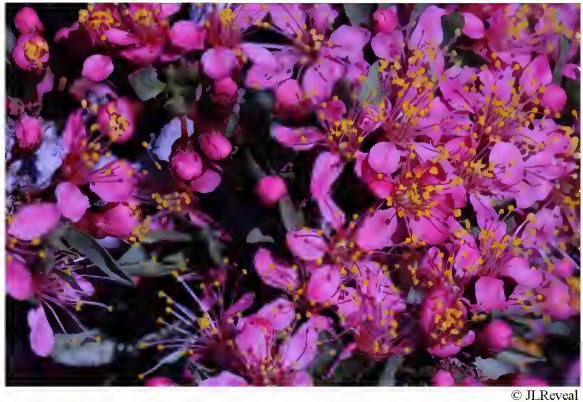

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Figure 19 *Prunus fasciculata* (Torr.) A. Gray

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Figure 20 *Calocedrus decurrens* (Torr) Florin

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Figure 21 *Chamaebatia foliolosa* Benth

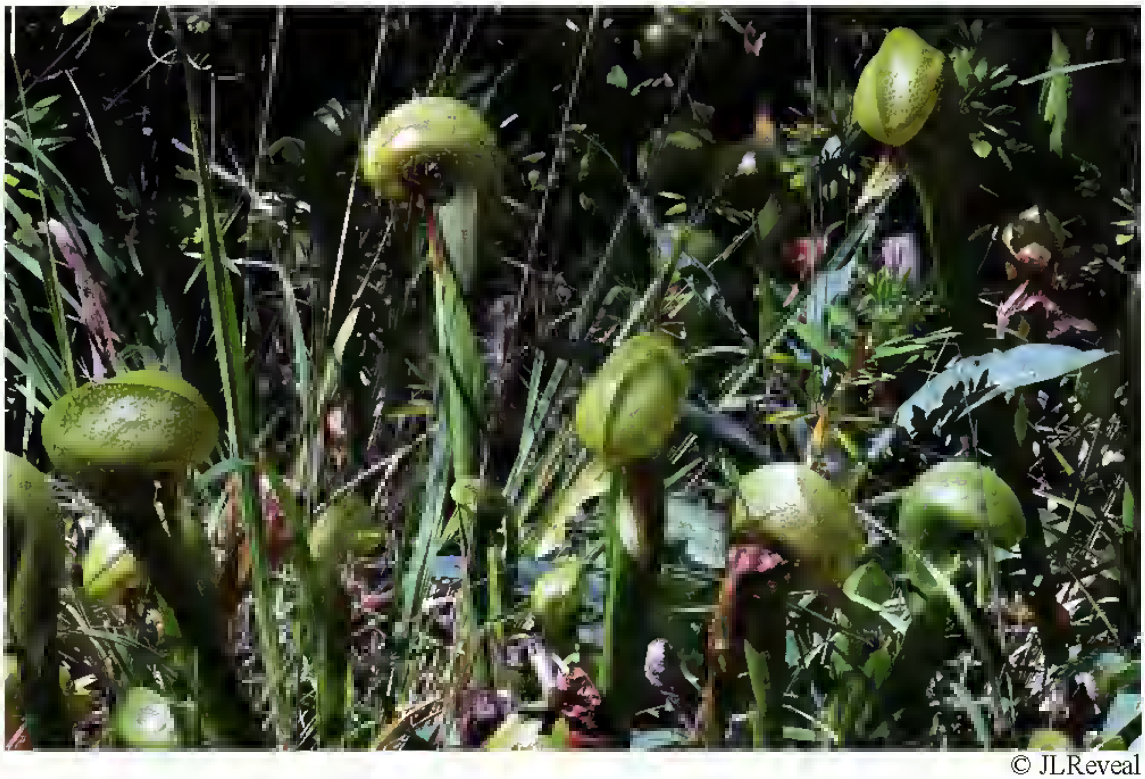

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Figure 22 *Darlingtonia californica* Torr

Following the two reports on Frémont's plants published in 1845, Torrey's interest became the collections of Major William H. Emory[46] whose *Notes on a Military Reconnaissance* was published in 1848 with an appendix by Torrey. Emory's route across the Southwest was hurried, but like Frémont, Emory sought to find new and curious plants. What is interesting about Emory is that he produced a series of sketch of plants which he gave to Torrey. These were of considerable value to George Engelmann[47] (1848, Fig. 24, below) of Saint Louis, who prepared the treatment of the cactus family, as the sketches provided a hint of the size and majesty of these difficult-to-collect plants. Even so, Emory wrote Torrey that his "numerous engagements" meant Emory's observations were limited.

The vagaries of the various editions of Torrey's appendix in the House and Senate versions of Emory's *Notes*, summarized by McKelvey (1955: 1014–1017), have long given botanists bibliographic nightmares (Barnhart 1895, Coville 1896, Farwell 1930) as the House and Senate versions differs not only in the plant's names and in the spelling of some scientific names but even in the number of published plates. Torrey's own copies give some hint to what is missing and otherwise were confused by the printers. Thus, Torrey's (1848a) names were first published in the Senate document (Feb–Apr) contrary to the information in Stafleu and Cowan (1976: 747), who list the House document (Mar–Jul, not "Feb–Jul") as the first place of publication (Torrey 1848b). Also, the first version of Executive Document 7 only consisted of 416 pages, later versions of this, and Executive Document 47, had 614 pages. At least Lieutenant James William Abert's[48] (1820–1897) observations of the vegetation of New Mexico (Abert 1848) were unhindered by human error, including Torrey's (1848c) list of plants in that report. The exchange of letters between Torrey and Emory in the archives of the New York Botanical Garden along with critical notes on the 72 known printed editions of Emory's *Report* in the botany library at the Gray Herbarium at Harvard University are critical to ascertain what was published and when (Fig. 23).

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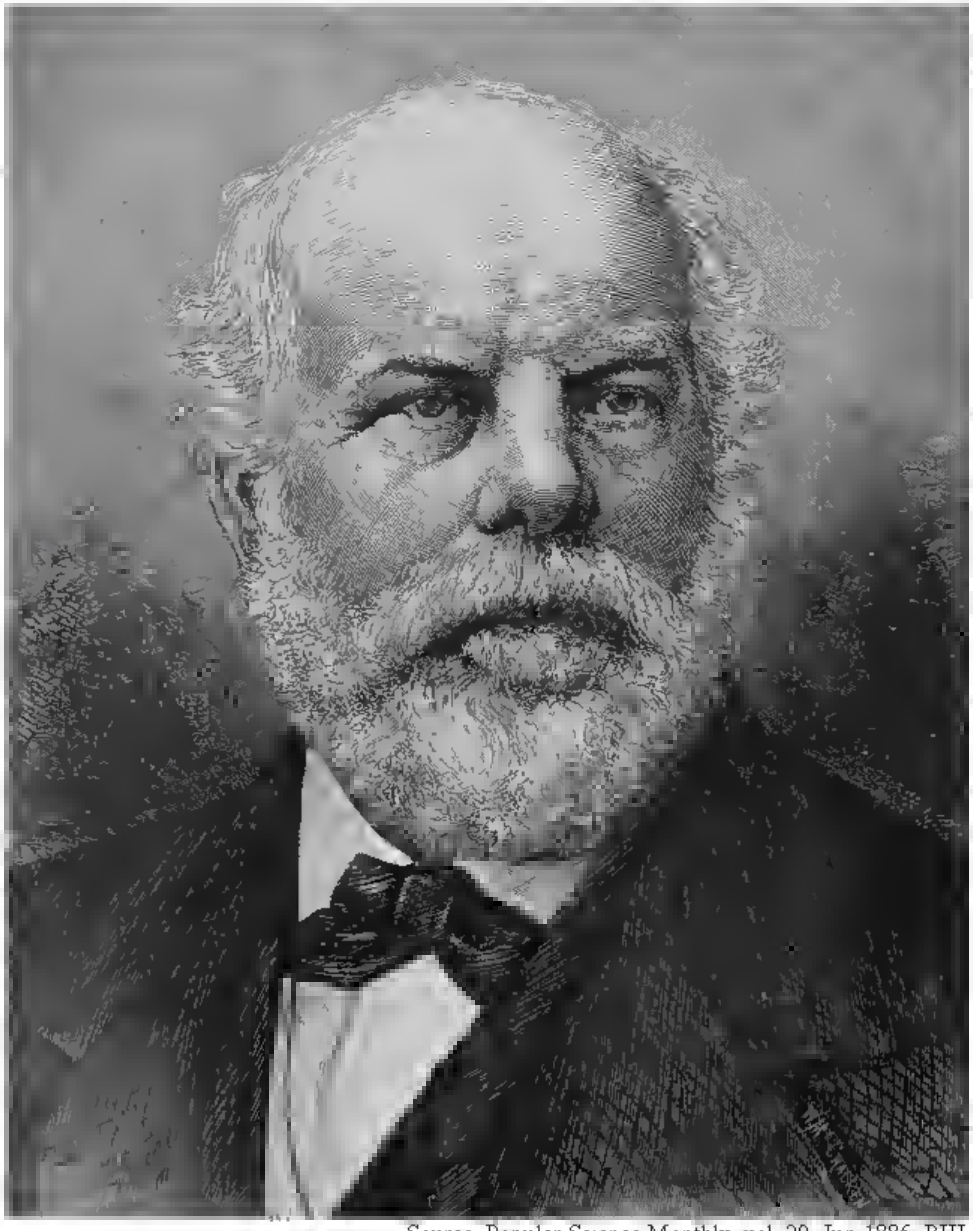
Figure 23. Inflorescence of *Sarcobatus vermiculatus* (Hook.) Torr.

The next two reports were equally troubled and the letters in the Archives at the New York Botanical Garden provide more evidence of Torrey's dissatisfaction with the results, both as to the publication and to the efforts of these new western expeditions. The new plants found by Captain Lorenzo Sitgreaves[49] and described in his *Report of an Expedition down the Zuñi and Colorado Rivers*, at least, were well prepared being collected by Dr. Samuel Woodhouse[50], a most capable surgeon/naturalist. The plates are excellent and illustrate for the first time such novel plants as two-needle pinyon (*Pinus edulis*; Fig. 25), desert trumpet (*Eriogonum inflatum*), and Gamble oak (*Quercus gambelii*, Fig. 26), all previously described by others. At least the Arizona walnut (*Juglans major*) proved to be new to science (Carvalho et al. 2012). As for Randolph B. Marcy's[51] efforts along the Red River (Marcy 1853, 1854a, 1854b), one can read what one can only say is the professor's suggestion (Torrey 1853c) that his explorer/students should do their homework: "It is remarkable that there occur[s] among your plants several species that were first discovered by Dr. James in Long's Expedition" this being slightly softened by the addition that some "have not been found since." Once again, the various editions, all prepared by local Washington printers, are fraught with errors, oversights and omissions to the point that in 1898 Frederick Coville, the foremost federal botanist of his day, called the Marcy report "a good illustration of the wasteful methods pursued in the publication of government reports."

The most successful of these early reports was that done again with the cooperation of Major William Emory. His 1859 *Report of the United States and Mexican Boundary Survey* (the second of two volumes) also marked Torrey's continued cooperation with Asa Gray (who worked as usual on the sunflower family and a few other groups) and George Engelmann whose knowledge of the cactus family (Fig. 27) was unchallenged. For a number of years Engelmann and Gray had worked on the Texas collections of Ferdinand Jacob Lindheimer[52], and their "Plantae Lindheimerianae", starting in

1845, resulted in a close working relationship between the two of them similar to what each had with Torrey. What marked this *Report* however, was the role played by the recently established Smithsonian Institution. Like most reports of the day, this one too contained a summation of the natural history, geology, and even aspects of new fields such as ethnology.



Source: Popular Science Monthly, vol. 29, Jun. 1886, BHL
Figure 24: George Engelmann

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Figure 25. *Pinus edulis* Engelm.

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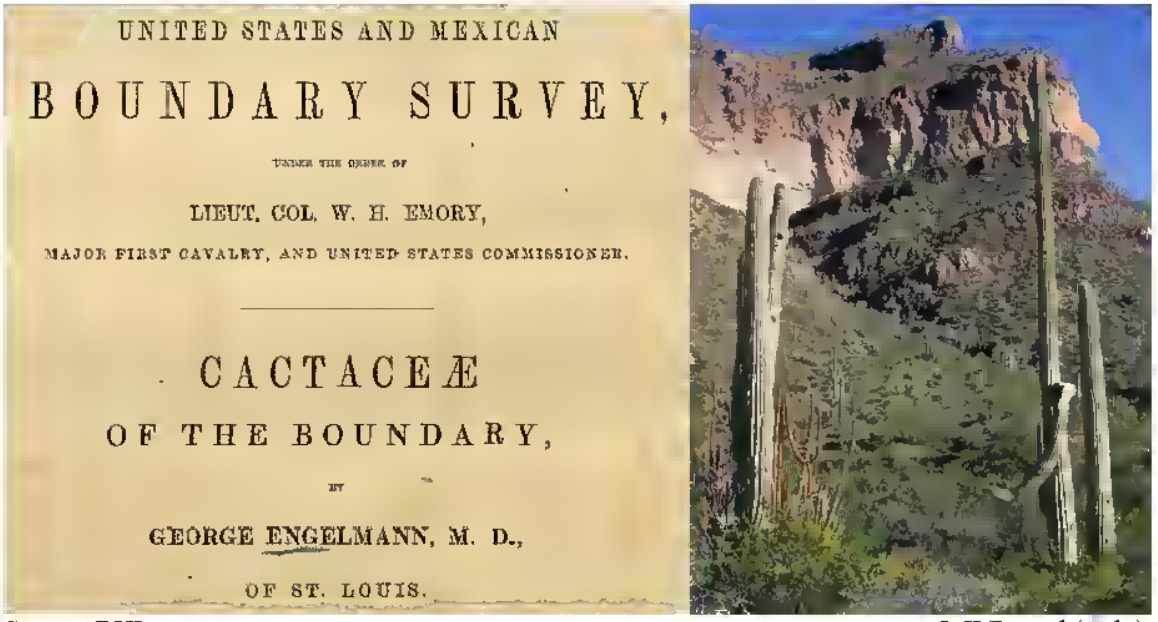
Figure 26. *Quercus gambelii* Nutt.


UNITED STATES AND MEXICAN

BOUNDARY SURVEY,

UNDER THE ORDER OF

LIEUT. COL. W. H. EMORY,

MAJOR FIRST CAVALRY, AND UNITED STATES COMMISSIONER.

CACTACEÆ

OF THE BOUNDARY,

BY

GEORGE ENGELMANN, M. D.,

OF ST. LOUIS.

Source: BHL © JLReveal (right)

Figure 27. Title page of Engelmann's 1859 treatment of the cacti (left), *Carnegia gigantea* (right).

Joseph Henry[53], Secretary of the Smithsonian (Fig. 28 left), a friend of Torrey from when Henry was at Princeton, had urged Torrey to join the Institution as botanist, but for numerous reasons as may be seen in their letters, their reunions in Washington were little more than occasional visits. Spencer Fullerton Baird[54], a colleague of Torrey and Gray's at the American Academy of Arts and Sciences (Fig. 28, right), accepted the position of assistant secretary and zoologist so that from 1850 onward Baird, Gray and Torrey were deciding who were to be the natural history collectors on the government expeditions. Because of them, highly skilled and well-trained naturalist were in the field. James Hall[55], like Torrey a member of the New York Survey, was involved with the selection of geologists. Hall had worked on Frémont's fossils, so it was natural that he continued to describe the new western fossils. With such collectors as Arthur Schott[56] (Fig. 29) and a former student of Torrey's, Charles Christopher Parry[57], the collections gathered during the Boundary Survey were superb (Fig. 30). Sixty-one plates were devoted just to botany with a host of others — many hand-colored — profusely illustrating Emory's *Report*. The treatment of the birds by Baird was a pivot point in academic ornithology for it put America in the forefront in this field.

Building a railroad across the nation dominated the 1850s. Where to build was a political question, not one of engineering or science, and yet the best Congress could do was to commission a series of railroad surveys across possible northern, central and southern routes in the hope that perhaps facts, rather than political interests, might select "the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean." In a rapid series of highly detailed expedition, eight reports were generated with the botany treated by Torrey and his associates.

Once again, the descriptions and plates were elegant, and the new plants plentiful. The "Railroad Reports" were the pinnacle of American natural history in the nineteenth century, and even the most casual review of the letters, images, and publications demonstrates both the hurried and yet critically careful work Torrey did to promote America's growing prominence in systematic botany even though the array of editions of the Reports and the variation in the entities published therein became a frustration to future generations of botanists[58]. This aside, there is no question that Torrey was at the pinnacle of his career as a botanist.

© Smithsonian Institution

Figure 28. Joseph Henry (left) and Spencer F. Baird (right).

Source: BHL

Figure 29. Native Americans illustrated by Arthur Schott.

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Figure 30 *Echinocereus engelmannii* (Parry ex Engelm.) Lem.

It was a fitting end to the era of Manifest Destiny. By 1861, when the last of the Topographical Engineers reports was published, the United States stretched from coast to coast. Western states were being added whenever the question of slavery could be resolved. Frémont stood for president of the United States in 1856 and lost to James Buchanan in a three-way race. Thomas Hart Benson died in 1858. Gray was becoming involved in the promotion of Charles Darwin's new theory on the origin of species — which Torrey did not accept — and Torrey's role in botany was declining as his duties as Assayer of the Mint become more and more demanding. So it was that Lieutenant Joseph C. Ives's *Report upon the Colorado River of the West* was published[59]. Again Torrey, Gray and Engelmann collaborated to produce a modest summary of the botany. The three men were aware of their duty and performed the task with care, but their heart and soul were much more committed to other efforts burdened by the fear that a war threatened the nation, an event they all recognized, that would fragment botanists as well.

The war years greatly curtailed botanical explorations and discoveries throughout the nation. Most of the newly discovered plants found after 1861 fell to Gray who rapidly replaced Torrey as the nation's foremost plant taxonomist with specimens flowing to Harvard instead of New York, the labors of the older generation were now moving on to a new one dominated by Gray.

The three botanical papers published by Torrey published after 1861 bespeak of his decline. The first was in the *Annals* published in 1867. He discussed a root parasite named *Ammobroma sonorae* by Torrey in Gray's 1854 "*Plantae novae thurberianae*". Today, sandfood is known as *Pholisma sonorae*. It looks more like a mushroom with small pinkish-purple flowers on the cap than a true flowering plant. The second paper, "A revision of the Eriogoneae" [sic, Eriogoneae] bears Torrey's name, but he wrote hardly a word. This paper, published in 1870, is considered one of the

best of the Torrey and Gray papers. The last appeared a year after Torrey's death. Much of the text had been written by Torrey, but it remained for Gray to rewrite, edit, and correct the original text, and so it was that the long-delayed report on the "Phanerogamia of Pacific North America" was published in Charles Wilkes's *United States Exploring Expedition* decades after it had any taxonomic significance.

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Figure 31. *Eriogonum watsonii* Torr. & A. Gray; its type was collected in the Humboldt Mountains of Pershing County, Nevada, by Torrey in 1865.

Torrey's gradual move away from the day-to-day demands of taxonomy was largely due to his new duties as Assayer, and the shift can be seen in his correspondence. He played a significant role in the development of the U.S. National Herbarium at the Smithsonian with many duplicates moving from his own herbarium to Washington. His travels were more numerous with frequent visits to Washington and elsewhere. By 1862 Torrey was living near Columbia College in New York City, and his herbarium was sold to the College in 1860 on the condition he could continue to use it. In 1865 Torrey sailed to California, and went overland to Virginia City in Nevada (figs. 31, 32). He was on business for the Secretary of the Treasury, but old habits were hard to break, and so he collected. A late spring trip to Florida in 1868 gave him an opportunity to see *Torreya* in the wild. He went westward again, in 1872, this time by train, stopping to admire from afar an honor bestow upon him by Charles Parry, his old student and faithful associate. His seventy-six years prevented him from climbing Torreys Peak but at 14,275 feet elevation, it was only three feet less than the adjacent Grays Peak about a mile away. Together, these high peaks in the Rocky Mountains stand as a fitting monument to the team of John Torrey and Asa Gray.

Torrey's life at the end and his legacy today

The final honors came late. Once settled at Columbia, the botanical world came to Torrey in informal gatherings, a kind of a botany club, and so it was that on December 2nd, 1867, the Torrey Botanical Club was born with John Torrey its first president[60]. In 1869, the Smithsonian Herbarium, still in Torrey's possession, went to Washington with Parry taking care of the transfer. Torrey hoped his young friend, now a well-established botanist would assume the curatorship, but alas that fell to another. Torrey's children were away, married with their own families. The sadness of his wife's death in 1855, smoothed over by his children, was eased somewhat by grandchildren, but botany was now reduced to a little collecting and an occasional meeting of an old friend he knew only from dried, flattened specimens. In time, even that lessened so that it was only meetings of the Torrey Botanical Club and an occasionally letter. In February of 1873 his "pleuritis" — for so it was called — worsened, and death came for John Torrey in his seventy-seventh year on March 10th of that year.

© JLReveal

Figure 32 *Mentzelia torreyi* A. Gray var. *acerosa* (M.E. Jones) Barney

The life of John Torrey remains a part of the history of botanical explorations and discoveries in the United States and especially in the American West. To read his letters, see his books, and touch his specimens is a privilege. Torrey's role in taxonomy remains fundamental to the mission of all botanists, especially at the New York Botanical Garden. Britton and Brown continued Torrey's work on the flora of the northeastern United States,[61] John Kunkel Small[62] botanized in the Southeast, and Per Axel Rydberg[63] matched Torrey's early work on the Rocky Mountains by writing floras of Montana (1900), Colorado (1906), the Rocky Mountains (1917) and then the Great Plains (1932). Torrey's work on the Pacific Northwest plants was matched a century later by the contributions of the Garden's Arthur Cronquist[64] to a series of illustrated volumes on the Pacific Northwest flora, and Cronquist also saw to the publication of the *Intermountain Flora*, its final volume published in 2012 by the Garden's botanists Noel and Pat Holmgren, with a little help from others.

What Torrey began nearly two century ago continues. The New York Botanical Garden, along with the Smithsonian Institution and the Missouri Botanical Garden, are at the forefront of botanical explorations and discovers in the twenty-first century. A *Flora of North America North of Mexico* continues to appear; Torrey would be pleased. And yet, even in an era of online resources and instant communication over the internet, the role of the herbarium for specimens and the library for real books remains first and foremost for here is where the real knowledge is stored. And, most importantly, that knowledge remains fundamentally tied to the out-of-doors and that is something no molecule or electron can ever replace.

End notes

[1] John Charles Frémont (1813–1890), *The Pathfinder*, was the first child of an affair between Anne Beverley Whiting Pryor and Charles Frémon, a French immigrant who was hired by the elder Major John Pryor (1750 –1823) in 1810 to tutor his teenage wife. The young couple fled Virginia and because Major Pryor's divorce petition was rejected by the Virginia House of Delegate, John was born out of wedlock, a fact that later would be a factor in Frémont's 1856 run for the presidency of the United States. Educated at the College of Charleston (1829–1831), he taught mathematics for the United States Navy before being appointed a second lieutenant in the newly formed Corps of Topographical Engineers charged with mapping the nation. Frémont's early expeditions were between the Mississippi and the Missouri rivers, so that when appointed to head his own expedition to the South Pass region of present-day Wyoming he was highly skilled in the tasks of recording both general and scientific observations. This quick trip in 1842 was followed by a second along the Oregon Trail in 1843, which took him to the Pacific Ocean and then south to California (Fig. 33), crossing the Sierra Nevada in January and February of 1844. Unlike other explorers of the period Frémont described, with Torrey, his own plants. Frémont returned to California again in 1845 and in 1846 became engaged in the Bear Flag Revolt, which resulted in the United States annexing the whole of Mexico's possessions in the Far West. His fourth expedition was privately organized and proved to be tragic, with the death of ten of his men in the snows of the southern Rocky Mountains. He briefly served as the military governor of California in 1847, and then was one of first two California senators, serving only a few months in 1850 and 1851. Frémont was the first Republican presidential candidate but placed second in the 1856 contest. Awarded the rank of major general during the Civil War, Frémont's war record was dubious and in 1862 he resigned and moved to New York. From 1878 until 1881 Frémont served as governor of the Arizona Territory, but soon he was destitute and died in 1890, living on the income from his wife's writings. For more information see Nevins (1955), Jackson and Spence (1970–1984), and Chaffin (2002). Frémont's correspondence with Torrey is in the archives of the Mertz Library at the New York Botanical Garden, Bronx, New York (Lenley 1973). See Herr (1987) for a biography on Jessie, and Herr and Spence (1993) for her letters. The short profile on Jessie by Petrulionis (2001) is excellent. For historical novels on the couple, see Stone (1944) and Denton (2009).

[2] Frémont actively collected plants along his entire route, gathering some 1400 specimens, but not all reached Torrey. A mule fell into a deep canyon in the Sierra Nevada with specimens gathered from the Columbia River to the Great Basin, but this loss was minor compared to a sudden flood that stuck the expedition in southwestern Kansas on their return in 1844. Water damage is obvious on many of the specimens in Torrey's herbarium at the New York Botanical Garden, and Torrey (1845: 311) reports "more than half of specimens were ruined before he [Frémont] reached the borders of civilization." Torrey and Frémont's "Descriptions of some new genera and species" along with four plates was published in Frémont's Report (1845: 311). For all of Frémont's botanical collection activities, see Welsh (1998).

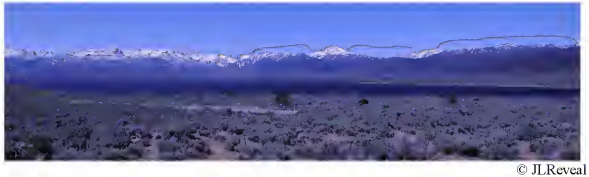

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Figure 33. Bridgeport Lake and Sierra Nevada from the foothills of the Masonic Mountains

[3] Isaac Sprague (1811–1895) is considered the best known of the early American botanical illustrators (Rudolph 1990). Born in Massachusetts he was self-taught, gaining considerable experience while serving as an assistant to John James Audubon (1785–1851) on an expedition up the Missouri River in 1843. A now rare bird, *Anthus spragueii*, or Sprague's pipit, was named for him by Audubon in 1844, who stated Sprague "shot it on the 19th of June, 1843, near Fort Union, Upper Missouri." While working on a book on the botanical collections of Meriwether Lewis and William Clark (Earle & Reveal 2004), I would occasionally spot the bird along the Missouri in eastern Montana. Sprague would illustrate many of Torrey and Asa Gray's new western species obtained during expeditions from 1838 to the mid-1850s. The original drawings may be seen at the Hunt Institute for Botanical Documentation at Carnegie Mellon University in Pittsburgh, at Harvard University, and a few at the New York Botanical Garden. The plant genus *Spraguea* was named for him by Torrey in 1853.

[4] "Plantae Frémontianae" (Torrey 1853) was a carefully crafted and beautifully illustrated report on the more elegant and impressive plants gathered by Frémont. Frémont's specimen of *Sarcodes sanguinea* (Fig. 1, above) was nowhere nearly as elegant as the Isaac Sprague illustration, but the details were there in the exactness few illustrators of the day could match. Years later Torrey saw the snowplant in a pot in a drug store window in San Francisco. In a letter to Gray, written a few weeks later on 31 July of 1865, Torrey expressed his amazement of a plant he knew only from Frémont's flattened specimen after seeing hundreds of them dotting the valley floor in Yosemite. His reactions were like those of others who first spy snowplant, pure wonderment! Isaac Sprague (1811–1895) was a noted botanical and zoological illustrator who worked for both John James Audubon and Gray. Working with George Lincoln Goodale (1839–1923) from 1876 until 1882, Sprague wrote *Wild Flowers of America*, published in parts of four plates and eight pages, with a summary volume published late in 1882 under a slightly different title with Alpheus Baker Hervey (1839–1931) as a co-author, and again under a third title in 1887.

[5] The article by Reveal and Reveal (1985) was, in part, a response to Lewis (1981). The Sweetwater Mountains are east of the Sierra Nevada in northern Mono County, California, and extend into portions of southern Douglas and Lyon counties, Nevada. The pieces of the carriage recovered by the United States Forest Service were found downslope from the site suggested in 1985; the pieces are housed at the office of the District Ranger in Bridgeport, California (see Wilusz 2011; Vogel 2012; Anonymous 2014; Graham 2014).

[6] The primary bibliography of John Torrey remains Rodgers (1942), followed closely by Robbins (1968); both have extensive reference sections. Details about the man were taken by both authors from Torrey's correspondence and writings at the Mertz Library; see "John Torrey Papers" (http://library.nybg.org/finding_guide/archv/torrey_ppf.html). The bulk of Torrey's correspondence was transferred long ago to the New York Botanical Garden by Columbia University. To the many works on Torrey cited by Stafleu and Cowan (1986: 401), two additional references can be mentioned here: Isley (1994) and Reveal and Pringle (1993).

[7] The history of Lyceum, detailed by Baatz (1990), is a review of The New York Academy of Sciences, as the Lyceum of Natural History would eventually be called stating in 1877. The eleven volumes of the *Annals of the Lyceum of Natural History of New-York* were published from 1823 to 1876.

[8] Amos Eaton (1776–1842) was the great popularizer of botany primarily because of the widespread use of his *Manual of Botany* (1817) which went through eight editions (1817–1840; see Stafleu and Cowan 1976: 718) in his life time. His misadventures with the New York legal system are discussed by Rodgers (1942: 13) and by Humphrey (1961: 78); see also Spanagel (2014).

[9] Although this work was attributed to all three members of a committee charged with writing the flora, only Torrey was its actual author. Yet, it is interesting that in the appendix there are descriptions of new plants by both Torrey and John Eatton Leconte, Jr. (1784–1860), the latter destined to be known for his expertise in entomology as well as botany (Barnhart 1917). Like Torrey, Leconte (also spelled LeConte or Le Conte) also attended Columbia College and was

schooled in botany by David Hosack (1769–1835; see Robbins 1964 and Sherk 2002) whose title was professor of theory and practice of physic. Hosack was the founder of the Elgin Botanical Garden and the author of *Hortus Elginensis* (1811). Leconte published a small track, *Catalogus Plantarum quas sponte Crescentes in Insula Noveboraco*, on the plants of Manhattan Island in 1811, but he is best known for his book, with Jean Baptiste Boisduval, *Histoire Général et Iconographe des Lepidoptérès*, which is famed for the many illustrations by John Abbot (1751–1841; see Calhoun 2007).

[10] Antoine Laurent de Jussieu (1748–1836), a French noble, was professor of botany at the Jardin des Plantes from 1770 to 1826 where, taking guidance from his uncle Bernard (1699–1777), he formulated the modern system of natural classification of plants in a series of lectures held over the years prior to his formal publication of *Genera Plantarum* in 1789 (Stevens 1994). By international agreement (McNeill et al. 2012), our modern names of plant families date from this work although some modern names were published before this date, and in fact one of de Jussieu's students, Jean François Durande (1732–1794), published most of his system in a text book some years before (1782) as did a competitor, August J.G.C. Batsch (1761–1802) whose best known work is *Dispositio Generum Plantarum Jenenstum* (1786).

[11] As may be seen by consulting Stafleu and Cowan (1979: 418), Edwin James (1797–1861) was long considered a minor footnote in western American botanical history. He is mentioned in many references (e.g., Pammel 1907–1908), but only two gave him real notice, the first being Ewan (1950: 13) and then McKelvey (1955: 211). The books by Goodman and Lawson (1995) and by Evans (1997) have done much to correct this oversight, especially when it comes to the natural history of the Stephen Harriman Long (1784–1864) expedition of 1820 to the Rocky Mountains. James wrote an account of his journey in December of 1822 and described several of his own species in 1825, with Torrey adding others in 1823 and 1824, before a full summary was presented three years later (Torrey 1826–1827).

[12] When President Thomas Jefferson (1743–1826) dispatched Zebulon Montgomery Pike (1779–1813) to find the headwaters of the Arkansas River, being the southern boundary of the Louisiana Purchase, he gave specific instructions that Pike was to thoroughly observe and collect natural history objects (Buckley & Harris 2012). These instructions were not unlike those given earlier to Meriwether Lewis in 1803. That Pike ignored them — collecting plants and animals being beneath the dignity of a military officer, and then getting himself and his men captured by the Spanish for crossing into Mexico — were minor offenses, it seems, to geographers. Pike did see the highest of the Colorado peaks, and indeed gave it a name, Grand Peak. After Edwin James climbed the peak, Stephen H. Long decided a more appropriate name would be James Peak. But alas, an honor like that, given to a lowly surgeon/naturalist, was not to last and so it was that Frémont altered the name to Pikes Peak (14,415 feet elevation) in 1840. Today, there is a James Peak (at a mere 13,294 feet elevation) named for Edwin James by the botanist Charles Parry (1862: 235); in 1862 Parry was the second person to climb Pikes Peak (Weber 1997).

[13] All of the species mentioned here were based on specimens collected by Edwin James and may be seen on the web at http://sciweb.nybg.org/science2/hcol/vasc/index.asp. However, an original specimen of the limber pine (*Pinus flexilis*) apparently never existed. For some unexplainable reason, the replacement type (a neotype) resides at Southern Illinois University with duplicates at Harvard University, Missouri Botanical Garden, Michigan State University, and the National Arboretum in Washington, D.C. (Andresen and Steinhoff 1971), but not at the New York Botanical Garden! One of the best known species found by James is the columbine, *Aquilegia coerulea* (Fig. 34), and except for the loss of color in the flowers, even today this is an exquisite specimen. One of James's new species that Torrey named was *Primula angustifolia*, a prized rock garden species. The best known of the grasses is what Torrey termed *Pleuraphis jamesii*, long known as *Hilaria jamesii* (Torr.) Benth. Its formal common name is "galleta grass" although among range management types the name "laughing jim grass" is frequently uttered. The type specimen gathered by James has an original illustration by Torrey added to the sheet.

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Figure 34. *Aquilegia coerulea* James

[14] The 1830 Lindley book *An Introduction to the Natural System of Botany*, was widely adopted. In addition to the 1831 American edition promoted by Torrey, a German translation (by Johann Bernhard Wilbrand [1779–1846]) was published in 1834, with a series of extracts presented by Carl Traugott Beilschmied (1793–1848) in the journal *Flora* in 1834. Even Lindley's key was translated by Beilschmied in 1832.

[15] The life and time of Asa Gray (1810–1888) was the subject of a senior thesis by A. Hunter Dupree (1959) and remains to this day the single best work on the man. Many of his letters were compiled and published in 1894 by his wife, Jane Loring Gray (1821–1909), and two volumes of his papers were assembled in 1889 by the first director of the Arnold Arboretum at Harvard, Charles Sprague Sargent (1841–1927). Stafleu and Cowan (1974: 983) have a long list of bibliographic notes on Gray, to which may be added the several papers recently published by Romero-González et al. (2010), including one by Reveal (2010). Gray's papers are at the Harvard University Herbaria (see: http://www.huh.harvard.edu/libraries/asa/ASABIO.html, where there is also a detailed chronology).

[16] Lewis David von Schweinitz (1780–1835), a member of the Moravian community in Pennsylvania, traveled widely in Europe as a young man before settling in Salem, North Carolina (1812–1821) and then in Bethlehem, Pennsylvania (1821–1835). Today, von Schweinitz is considered to be the "patron saint" of North American mycology (Rogers 1977), his herbarium of some 23,000 specimens (mostly fungi) is at the Academy of Natural Sciences in Philadelphia. Stafleu and Cowan (1985: 437) provide a rather full listing of references about him. The discussed crytogamic flora was published by von Schweinitz alone in 1821. The authorship of the late 1825 von Schweinitz monograph of *Carex* must be noted. The title given in the *Annals* is as given in the Reference section of the present work (see Schweinitz 1825b), but in the table of

contents the authorship is cited as "L.D. De Schwinitz and J. Torrey" and there is (on page 374) the following message to the Committee of Publication from von Schweinitz dated December 20, 1825:

> The Monograph of the Carices, in its present shape, differs so essentially from the unfinished materials, which, on my departure for Europe, I confided to my friend Dr Torrey, with a request to make such use of them as he deemed proper, that it would be an act of injustice to that gentleman to consider him simply in the light of an editor The judicious and elaborate amendments he has proposed, and the mass of new and valuable matter he has added, entitle him to a participation in the authorship of the work. I am anxious, therefore, that the Monograph should be considered and quoted in all respects, as the joint production of Dr. Torrey and myself.

Although the modern rules of nomenclature (McNeill et al. 2012) mandate that the authorship must be that given in the original publication, Art. 46.9 does allow external evidence to be used to determine authorship, and so it is that the few new names published in late December of 1826 are now treated as "Schwein. & Torr." The majority of new names suggested by Torrey to Schweinitz as well as those newly recognized by him were published in an earlier volume of the *Annals* (Schwinitz 1824).

Schweinitz is also known for his study of *Viola* (1822) and his summary of the Thomas Say collection of plants from the Old North West (1825a). His final work was on the fungi of North America published in 1832 (see Rogers 1977: 238).

[17] Chester Dewey (1784–1867), then at Williams College, ultimately moved to Rochester, New York, in 1836 and took a position at the Collegiate Institute of Rochester, ending his career as professor of chemistry and natural philosophy at the University of Rochester (Stafleu and Mennega 1998: 255; Seelve 1900). Aside from his numerous papers on *Carex* in the *American Journal of Sciences and Arts* and elsewhere, his 1840 *Report on the Herbaceous Flowering Plants of Massachusetts* is noteworthy as he adopted Lindley's arrangement of families.

[18] Gray's 1873 obituary is available online at http://www.huh.harvard.edu/libraries/Gray_Bicent/gray_torrey.htm with a number of images. The quote about Dewey is on p. 415.

[19] See Rodgers (1942: 91).

[20] See Rodgers (1942: 97), quotes taken from a letter to von Schweinitz.

[21] William Jackson Hooker (1785–1865) was one of the foremost botanists in England and became an important correspondent of John Torrey's. Hooker's primary work of interest to Torrey was *Flora Boreali-Americana*, which was published in 12 parts from 1829 to 1840. Hooker and George Arnold Walker Arnott (1796–1868) jointly authored *The Botany of Captain Beechey's Voyage*, which included stops along the Pacific Coast of North America in 1826, 1827, and 1828 (McKelvey 1955). As a prolific author and editor (Stafleu and Cowan 1979: 283), numerous North American plants came to his attention, and it was through Hooker that both Torrey and Gray received specimens made by European botanists that were critical to the Americans own monographic and floristic efforts. Like Torrey, Hooker worked on cryptogams, ferns, conifers, and flowering plants. For more information on Hooker see J.D. Hooker (1902) and Allan (1967).

[22] David Douglas (1799–1834), a Scottish botanist and collector, is probably the best known of the early western naturalists and his plant specimens were critical to Torrey and Gray as they wrote their *Flora*. His adventures have been widely documented as noted by Stafleu and Cowan (1976: 674) who failed to mention a 1962 episode, "The Grass Man", on the television series *Death Valley Days*. Stafleu and Mennega (2000: 66) account for much of the more recent literature, to which may be added a few recent books (House and Mitchell 1999; Bown 2002; Mitchell et al. 2005; Nisbet 2009). Two earlier books not mentioned in 2000 are those by Spongberg (1990) and Reveal (1992). Of critical importance to Douglas's early explorations in

the Pacific Northwest is his journal (Douglas 1914) published 70 years after his untimely death in Hawaii.

[23] André Michaux (1746–1802) was an adventurous French botanical collector who explored much of eastern North America from 1785 until 1796, gathering primarily plants of potential horticultural or naval stores value for the French government (Deleuze 1804, 1805; MacPhail 1981; Savage and Savage 1986; Taylor et al. 1998; Taylor and Norman 2002; Baranski 2004). For a portion of the time, he collected with his son Francois André (1770–1855, F.A. Michaux 1805). *Flora Boreali-Americana*, published in 1803, was the first major treatment of the native plants of the region. The beautifully illustrated work on oaks (Michaux 1801, 1810), followed by the three volume work on North American trees by François (Michaux 1810–1813), are among the best of the early illustrated works on the forest trees of North America. There is no evidence that Torrey received any of Michaux's original American specimens, however.

[24] George Bentham (1800–1884), an English gentlemen and famed botanist, was a frequent correspondent with Torrey (Lenley 1973). He published many new species of North American plant sent to him by Torrey (see Stafleu and Cowan 1976: 173; Jackson 1906; Isley 1994).

[25] Robert Brown (1773–1858) was the best known of the English naturalists when Torrey visited England (see Stafleu and Cowan 1976: 364; Mabberley 1985).

[26] Moses Ashley Curtis (1808–1872) is best known as a mycologist and a correspondent with von Schweinitz (Petersen 1980; Berkeley 1986). He made a number of contributions on the cryptogams in the 1840s and 1850s for reports on the explorations of the American West.

[27] Hardy Bryan Croom (1797–1837) died in the breakup of a passenger steamboat off Cape Hatteras (Hale 1837; Redfearn 1935; Flowers 1979; Rogers and Clark 1999; Conrad 2011), but in spite of his short life he is known today for the genus *Croomia* named by Torrey in 1840. Letters from Torrey to Croom are preserved in The Southern Historical Collection at the University of North Carolina. Croom's 1833 *Catalogue*, published with Henry Loomis, was revised and published again in 1837 with the help of Torrey. Croom's paper on *Sarracenia* (Fig. 35) was published in the *Lyceum* in 1837.

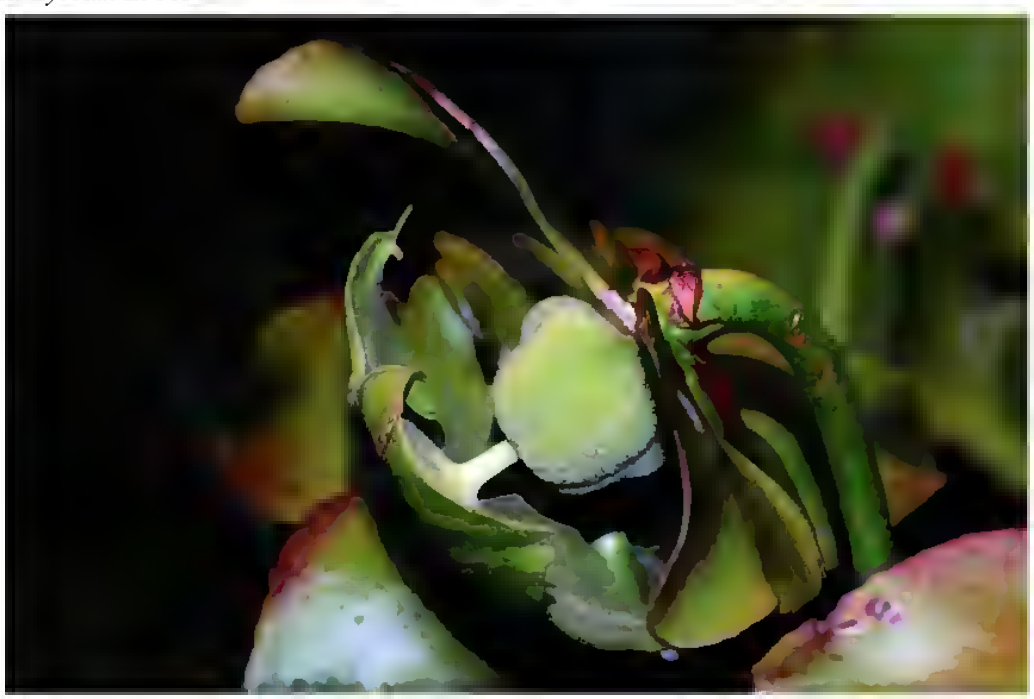

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Figure 35. A flower of *Sarracenia purpurea* L. in early fruit.

[28] John Leonard Riddell (1807–1865) was broadly interested in natural history, and like most of his contemporaries he took a medical degree in 1836 and then spent the remainder of his life at the Medical College of Louisiana (now Tulane University). Also, like Torrey, Riddell was associated with a mint (at New Orleans), but unlike Torrey, Riddell (1847) was also a science fiction writer. Botanically, Riddell is best known for his collecting activities in eastern Texas (Stafleu and Cowan 1983: 784). Two works were important to Torrey, his 1835 "Synopsis of the flora of the western states" and Riddell's now famous "Catalogus florae ludovicianae," published in 1852 and 1853, which supposedly was supported by specimens and illustrations sent to the Smithsonian Institution. Originally, the manuscript was sent to Gray, who suppressed its publication but apparently kept some of the collections (Ewan 1967: 45). The taxonomic significance of the long-ignored 1852–1853 publication in the *New Orleans Medical and Surgical Journal* was reviewed by Wilbur and Whitson (2005, 2007).

[29] Constantine Samuel Rafinesque (1783–1840) is without doubt the single most interesting, and controversial, naturalist in North American history (Boewe 1982, 2005, 2011). An acknowledged genius with exceptional abilities, he is also credited with being one of systematic biologists most destructive, especially when it comes to nomenclature (Kastner 1977; Flannery 1998). After a three year visit to America (1802–1805) as an apprentice in a mercantile house in Philadelphia, he returned in 1815 only to lose all of his books, collections, and manuscripts in a shipwreck off the coast of Connecticut. His interest in American natural history began much earlier when he approached Thomas Jefferson in 1804 to obtain an appointment as a naturalist for the 1806 Freeman-Custis expedition along the southern border of the Louisiana Purchase. He was passed over in favor of Peter Custis (1781–1842), who proved to be singular unsuccessful at the task although his observations of the vegetation were critical (Morton 1967; Flores 1984). When Torrey first met Rafinesque he was much more reasonable, at least in terms of nomenclature, and the two men developed a close relationship, especially since Rafinesque had a professional relationship with Dr. Samuel Latham Mitchill (1764–1831; Aberbach 1988), whose prominence in medicine, natural history, and politics was well established, and as the owner of the journal *Medical Repository*, allowed Rafinesque a ready avenue to publish his findings. Torrey and Rafinesque collected together, but upon Rafinesque's return from a personal trip into the Allegheny Mountains in 1818, his suggestion that he found more than 250 new species must have caused Torrey some concern. The relationship between the two soon dimmed, especially in the 1830s when Rafinesque, already a prolific author (Stafleu & Cowan 1983: 549), proposed hundreds of new genera and species of little or no merit in Torrey's view, so that finally Torrey and Gray essentially ignored what Rafinesque wrote — a view largely adopted by others until the 1970s. When Merrill (1949) finally compiled Rafinesque's botanical efforts he showed that Rafinesque proposed nearly 2700 new generic names and more than 6700 species in about 1000 publications. Unfortunately, only a few of Rafinesque's types exist today as his herbarium was basically destroyed after his death (Stuckey 1971).

[30] Charles Wilkins Short (1794–1863) was one of the most prolific of Torrey and Gray's many correspondents, and letters from both botanists are found in Short's archives at the University of North Carolina (in the Southern Historical Collection). Like Rafinesque, Short was also associated with the Transylvania and the Filson Club, as mentioned by Stafleu and Cowan (1985: 568). Short's work, "Florula lexingtoniensis," published in 1828 and 1829, was the basis for his 1833 "Catalogue" published with Robert Peter (1805–1894) and Henry A. Griswold, with a series of supplements following until 1840; see Stuckey (1978) for a detailed analysis.

[31] Thomas Nuttall (1786–1859) was the single most important source of new information on North American plants for Torrey and Gray. The life and times of Nuttall are reviewed in detail by Graustein (1967) and Ewan (1971), with information on his travels into the Old Northwest by Graustein (1957), his ascent of the Arkansas River by Lawson (2004), and his trans-Mississippi travels by McKelvey (1955) and more recently by Williams (2003). Nuttall came to North America in 1808 and went westward for Benjamin Smith Barton (1766–1815) in 1810, and then

ascending the Missouri River in 1811 (Reveal 1968; Fig. 36). Nuttall's *Genera of North American Plants*, published in 1818, served Torrey well in his own early works, and Nuttall's later *North American Sylva* (1842–1849) replaced the earlier work of François Michaux (see Stafleu and Cowan 1981: 781). Nuttall provided Torrey and Gray with numerous manuscript names that were published in their *Flora*, crediting the names to Nuttall, or modifying the descriptions. Nuttall is also well-known for his work in ornithology, being honored in 1873 with the establishment of the Nuttall Ornithological Club, the oldest such group in the United States.

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Figure 36. *Eriogonum flavum* Nutt. (left), *Rudbeckia columnifera* (Nutt.) Wooton & Standl. (right, digital painting), both collected by Nuttall in 1811 and named in 1813.

[32] Nuttall left Harvard when Nathaniel Jarvis Wyeth (1802–1856), a Boston merchant, convinced him to go to Oregon in 1834. While many of Nuttall's new western plants were accounted for by Torrey and Gray, Nuttall (1834a, 1834b, 1840-1841, 1842) published several papers and left a multitude of specimens at the Academy of Natural History in Philadelphia. A provision in an uncle's will mandated that Nuttall reside in England at least nine months each year so that Nuttall returned to America only once (1847–1848), where he published two papers with many new western species (Nuttall 1848a, 1848b). In 1832 Wyeth collected numerous new species in western Montana, southeastern Idaho, and elsewhere along his route, one being *Iris missouriensis* (Fig. 13, above). Nuttall's own discoveries were far more numerous. For more information on Wyeth and Nuttall see McKelvey (1955) and especially Graustein (1967).

[33] The rise of botany in general education can be traced to Phelps (1833b) for young women and to Eaton for young men. Lincoln's (nee Phelps) book underwent two major revisions (1845, 1853) with 39 printings (Rudolph 1984). Her *Botany for Beginners* saw 27 printings. Eaton's 1820 *Botanical Exercises* introduced botanical laboratories into college curricula (Rudolph 1996). Gray's 1836 *Elements* was revised and renamed *The Botanical Text-book* in 1842 and went through six editions and numerous printings (Stafleu & Cowan 1976: 986).

[34] The history of early scientific exploration and discoveries in western North America was summarized by Goetzmann (1959, 1966, 1986). The earlier trilogy by Bernard De Voto (1943, 1947, 1952), takes a larger view and covers a broader period. The role of scientists in the West was reviewed by Reveal and Hafen (1970). The classical work on the fur trade remains Hafen's (1965–1972) ten-volume work on the subject.

[35] The best resource for these collectors remains McKelvey (1955; see in particular her bibliography) although brief summaries of many of these naturalists are provided by Thomas (1969), Reveal (1992), Reveal and Pringle (1993), and Beidleman (2006). The classical work on Chamisso (Lentzner 1893) remains still the best source of information on this naturalist, who is better known for his poetry. The life of Alexander Collie, who resided in Australia from 1831 until his death in 1835, was summarized by Chessell (2008). Beechey's (1832) account of his visit to California is detailed and the western American botanical discoveries by Collie and Lay were dealt with by Hooker and Arnott (1839). Bentham (1844–1846) described the plants found by Hinds. Tolmie's journals are now available, being published in 1963; see also Lamb (1982).

[36] Thomas Hart Benton (1782–1858) was *the* advocate in the Senate for westward expansion throughout his five terms (1821–1851) and he was a major, behind-the-scene force, supporting western exploration by the U.S. Army and early enthusiasm for an intercontinental railroad from the Atlantic to the Pacific. Torrey, well aware of the power Benton had in the Senate, no doubt "allowed" Frémont to author the new species collected by Frémont as a means of ensuring Benson's continued support of future western explorations.

[37] Christopher Houston Carson (1809–1868), mountain man, trapper, and guide, is equally well-known today as a western frontiersman and a pulp-fiction hero (Averill 1849) as well as a character in comic books, movies and a television series. Separating fact from fiction is not always easy, but for Frémont, Carson was the perfect man for the task of trekking from Missouri to California. Frémont would name many places for his guide; today, the best known is Carson City, the capitol of Nevada. Of the numerous scholarly books about Carson the more recent are by Carter (1968), Dunlay (2000), Roberts (2001), Remley (2011), Sides (2006), and Simmons (2003); many of Carson papers are at The Bancroft Library at the University of California.

[38] The Bear Flag Revolt was a brief (10 June to 9 July 1846) armed revolt against the Mexican government in Alta California carried out by a small group of Americans with the aid of Frémont. After the Revolt, the battle for California was taken over by Frémont and Commodore Stockton (see below) while awaiting arrival of the U.S. Army under the command of General Kearney (see below). Not surprising, throughout this period Frémont continued to collect plants.

[39] Robert Field Stockton (1795–1866) joined the U.S. Navy in 1811 and served initially in the War of 1812. He resumed his career in 1836 and being a member of a political family — his father was a senator from New Jersey — young Stockton was soon offered the position of U.S. Secretary of the Navy in 1841 which he declined. After serving in Texas (1844–1846) he took command of the Pacific Squadron and aboard the *USS Congress* he soon was involved in the conquest of California, ultimately commanding the relief command that saved Major Kearny and his dragoons at the Battle for San Pasqual (December 1846). Just prior to this Stockton appointed Frémont military governor of California (see endnote 40, below). In 1851, Stockton was elected to the Senate serving just as Frémont was leaving his brief tenure as a senator from California.

[40] Stephen Watts Kearny (1794–1848), like others of his generation, served in the War of 1812, but was soon in the West, being a member of an 1819 expedition along the Yellowstone River in Montana and Wyoming and another in 1820 along the Missouri River (Kearney 1908). He returned in 1825 on another expedition (Atkinson 2000) prior to assuming the command of a military barracks near St. Louis in 1826. In 1836 Kearny took command of the 1st Dragoon Regiment and was stationed at Fort Leavenworth charged with the task of protecting the western frontier by providing military protection for wagon trains crossing the Great Plains. His Army of the West was assigned to Santa Fe with the charge of establishing a joint civil and military government. Interestingly, each of the subcommanders was assigned the task of collecting

natural history objects, with the plants going to Torrey for identification. When he reached San Pasqual in southern California, his men were trapped and relief came in the form of Kit Carson alone and a small command of Stockton's marines. Both Kearny and Stockton were of equal military rank, but who was supreme was not defined. Frémont, being of lower rank and already appointed the military governor of California by Stockton, initially refused to abandon his duties whereupon he was order to Washington to face a court marshaled for insubordination and disregard of orders.

[41] Publication of "Plantae frémontianae" in April of 1853 was a singular effort combining the field work of a member of the U.S. Army's Corp of Topographical Engineers (Frémont), the critical analysis by an American botanist (Torrey), and the artistic skill of an illustrator (Issac Sprague). In many respects this would establish the minimal requirement for publication of new names of western North American plants over the next two decades. Besides the snowplant (*Sarcodes sanguinea*, Fig. 1, above), Torrey's *Carpenteria californica* (tree anemone) and *Coleogyne ramosissima* (blackbrush) are still recognized with *Spraguea umbellata* now assigned to *Cistanthe* and Torrey's new shrub genus, *Emplectocladus fasciculata* (Fig. 19, above) placed in *Prunus*. Although Frémont saw incense cedar in February of 1844 and collected a specimen, it is likely that the majority of the gathering was damaged in a river flood in Kansas on Frémont's return trip so that Torrey had in hand only a few fragments of the tree. As a result when the species was described in 1853, Torrey used as the basis of his description, and the published illustration, a Gilbert White Hulse (1807–1883) gathering from northern California obtained in 1850. Welsh (1998: 303) designated the fragments obtained by Frémont as the "holotype" (actually a lectotype). While his choice was unfortunate, the few fragments are not ambiguous the typification must stand, and no epitype is necessary.

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Figure 37. *Psathyrotes annua* (Nutt.) A. Gray

[42] Naval Lieutenant Charles Wilkes (1798–1877) was given the command of the United States Exploring Expedition in 1838, the American equivalent of the many, earlier around-the-world expeditions long-sponsored by European governments. Like the expeditions of England's James Cook (1728–1779), and especially the first abroad *HMS Endeavour* (1768–1770), the Wilkes Expedition included naturalists and artists for the sole purpose of collecting and documenting natural objects as well as naval personnel capable of carrying out the primary purpose of conducting detailed naval surveys (Henderson 1953; Tyler 1968; Barkan 1987; Philbrick 2003; Blumenthal 2009). Gray's 1854 summary of the botany of the Expedition only had a limited printing of 100 copies of which 21 were lost in a fire; a run of 150 copies was unofficially printed in New York (Stafleu & Cowan 1976: 991). A second report by Gray, issued in 1856, was composed of 100 plates, and again there were both official and unofficial printings.

[43] Carl ["Charles"] Andreas Geyer (1809–1853) was a German botanist who collected in the United States on the Mississippi and Missouri rivers from 1842 until 1843 mainly with Joseph Nicolas Nicollet (1786–1843). Nicollet, formerly a professor of mathematics and an astronomer in his native France before immigrating to the United States, was an ideal choice to make corrections to the already existing maps of the area. Geyer was personally employed by Nicollet and, without an explanation, Nicollet stated in his report that "owing to the loss of a case containing near one-half of my original collection" the summary given by Torrey (1843a) was limited (McKelvey 1955). Engelmann (1843) also comment on Geyer collections from Illinois and Missouri. Upon completion of his employment with Nicollet, Geyer went west, initially with Sir William Drummond Stewart in 1843 (Porter & Davenport 1963; Benemann 2012), gathering plants that made their way to Hooker who arranged for their sale and accounted for the new species (Hooker 1847, 1851, 1853, 1855, 1856). Geyer (1845–1846) wrote an account of his travels mainly in the West. Likewise, his activities, especially in the Pacific Northwest, were recorded in letters and journals written by others, which reveal a great deal about the temperament of the man, all of which is summarized not always in a kindly way by McKelvey.

[44] Curiously, the copy of the report now in the Mertz Library at the New York Botanical Garden is the later (1845b) printing. As several of Torrey's original volumes are now in private hands, the missing 1843 volume may well be one of those.

[45] The Mertz Library has a series of detached *Annual Reports of the Geological Survey of New York* published by Torrey including one in 1840 and another from 1849. Clinton published supplements in 1865 and 1866, as did Peck in 1867, with minor reports appearing regularly until 1913. There is also an 1848 paper by Lee on medicinal plants. No doubt several of these early papers were used by Torrey to compile his 1853 report.

[46] William Hemsley Emory (1811–1887) was a noted explorer mainly in Texas and later along the newly established border of the United States and Mexico (Norris et al. 1998). He was born of an established family of modest wealth in 1811 at Poplar Grove, an old estate in Queen Anne's County, Maryland, dating back to the 1660s (Goodheart 2008). Educated at West Point (he graduated in 1831), his early years in the army were uneventful until he began a career of mapping the United States border, first the Canadian (1844–1846) and then the Mexican (1848–1853). Although Emory went to California with Kearney, he was impressed by the vegetation and routinely collected plants not only then (Emory 1848) but later when he directed the United States and Mexican Boundary Survey (Emory 1858–1859; McKelvey 1955). Emory was forced to retire from the Army in 1876 and died in 1887.

[47] George Engelmann (1809–1884), German by birth but American throughout his professional career as a physician and botanist, resided in Saint Louis from 1835 onward except for a brief visit to his native country in 1840, where he married, and two additional voyages to Europe in 1857 and 1868 that were entirely botanical. His interest in botany began early and even his dissertation for his medical degree (Engelmann 1832) was more on botany than medicine. In 1842 he published his monograph on *Cuscuta* (revised in 1860) and began his study of the cacti, a group readily conceded to him by Torrey and Gray. It was only late in his life (1879) that Engelmann

actually went west mainly to continue his study of conifers (Engelmann 1880). For most of his botanical career, Engelmann was more commonly associated with Gray than Torrey. Also, he concentrated his efforts mainly on collections of plants made by fellow Germans in Texas and Mexico (Geiser 1937, 1948), and with various collectors in the Rocky Mountains (Ewan 1950; Isley 1994).

Source: BHL

Figure 38 View of the Santa Fe mission and Fort Marcy (background) by J.W. Abert

[48] James William Abert (1810–1897), the son of John James Abert (1788–1863) who was the head of the Corps of Topographical Engineers, joined the Corps in 1843 and was soon in the field on Frémont's third expedition and then, in 1846, with Kearney. Frémont assigned the task of completing the mandate of his third expedition to Abert, and in the process Abert collected natural history objects (Goetzman 1959). He did the same with Kearney (Abert 1848). For the published reports of both Frémont and Emory, Abert provide numerous illustrations (Fig. 38) and after the Civil War and his retirement from the U.S. Army, he taught drawing at the University of Missouri.

[49] Lorenzo Sitgreaves (1810–1888), a graduate of West Point in 1832, was assigned to Virginia only to resign and study civil engineering so that when he rejoined the U.S. Army in 1838 he became a member of the Corps of Topographical Engineers, surveying the Canadian boundary (1839–1841) and then in Louisiana and Texas (1841–1842) before going to the main office of the Corps in Washington, D.C. His only major western expedition was the survey of the Zuñi River in 1851, although he was involved in the war with Mexico (1846–1848). In ill health, Sitgreaves served as a mustering officer during the Civil War, retiring from the Army in 1866.

[50] Samuel Washington Woodhouse (1821–1904) was a skilled physician and naturalist who was assigned in 1849 to survey the boundary of the Creek Nation with Lorenzo Sitgreaves in the Indian Territory of modern-day Oklahoma (Woodhouse 1992). Woodhouse was especially interested in birds and made numerous specimens that gradually made their way to ornithologists in Washington and Philadelphia. His botanical specimens were given to Torrey to evaluate. As the expedition's physician, he treated himself in 1851 when he was bitten by a rattlesnake and

later when wounded by an arrow in a skirmish with local Indians along the Colorado River (Woodhouse 2007). A small number of plants (e.g., *Picradeniopsis woodhousei*) and animals (e.g., *Bufo woodhousei*) were named in his honor. The Woodhouse scrub-jay (*Aphelocoma woodhousei*) ranges from the northern Great Basin to Sonora and Chihuahua in Mexico.

[51] Randolph Barnes Marcy (1812–1887) was a graduate of West Point and spent his entire professional life as a military officer serving first in the so-called Black Hawk War of 1832 and in the war with Mexico in 1846. He was an officer on an expedition in 1857 to confront the Mormons of Utah. All of this first-hand experience in the West, including a perilous journal across the Rocky Mountains in the dead of winter in 1858, resulted in a book entitled *The Prairie Traveler* which, like Frémont's writings before him, became a well-known guide to the trails and dangers of crossing the deserts and mountains of the West. Most of his notable efforts were after his 1852 expedition to the headwaters of the Red River in Colorado that Pike had failed to locate in 1806. One of his officers was George B. McClellan, who later won fame as a general during the American Civil War and married Marcy's daughter, Ellen Mary, in 1860.

[52] Ferdinand Jacob Lindheimer (1801–1879, Fig. 39) is one of the more remarkable characters on the botanical frontier of the American West, and especially in Texas (Lich 1996). Born in Frankfurt, Germany, and schooled at the University of Bonn, he was politically active on the losing side of a reform movement and consequently emigrated to the United States in 1834, settling briefly in New Orleans before moving into Texas and then into northern Mexico only to depart from there in late 1835 as the so-called Texas Revolution was starting. It seems that Lindheimer arrived one day after the Battle of San Jacinto (21 April 1836), in which Sam Houston (1793–1863) and his band of Texan colonists routed the Mexican forces led by General Antonio López de Santa Anna (1794–1876) in a battle lasting just 18 minutesand that resulted in the death of more than 600 Mexican soldiers. Following the war, Lindheimer resigned from the army (in 1837) in response to a query by Engelmann, and after residing in St. Louis during the winter of 1839-1840, he took up the task of seriously collecting plants — an effort that was to last for the next 13 years — sending specimen to Engelmann, Asa Gray, and even to botanists (via the sale of his large sets of specimens) in Europe, the most notable being G.H. Adolf Scheele (1808–1864) who published several new species in an 1849 issue of the journal *Linnaea*.

Source: Wikimedia Commons

Figure 39. *Oenothera lindheimeri* (Engelm. & A. Gray) W.L. Wagner & Hoch

[53] Joseph Henry (1797–1878) was a founding member of the National Institute for the Promotion of Science which was organized in Washington, D.C., in 1840 and, as an organization, served as the precursor to the Smithsonian Institution which was founded in 1846. As a member of the Institute, Henry, then at Princeton, urged that this organization house the natural history collections made by Charles Wilkes and others during the United States Exploring Expedition, an around-the-world expedition that lasted from 1838 until 1842. Although funding for a national museum was provided to the United States via the will of James Smithson (1765–1829), the some $500,000 was the subject of a prolonged and often bitter partisan debate in Congress as to what was meant by Smithson's request that the money be used "for the increase and diffusion of knowledge" (Ewing 2007). As the Smithsonian Institution's first Secretary, Henry established the focus of the organization as the nation's leading scientific center and repository for all government-sponsored collections. Henry served as Secretary until his death (Moyer 1997).

[54] Spencer Fullerton Baird (1823–1887), like John Torrey in botany, basically ruled zoology in terms of the collecting and naming of animals found in the United States, and especially those gathered on federally sponsored expeditions. Torrey knew Baird as a student at the College of Physicians and Surgeon. When Baird left Dickerson College and went to the Smithsonian in 1850, he reportedly brought two box-cars of books and specimens, thereby strengthening the Institution's scientific holdings; by the time he died, the Smithsonian had more than two million items largely due to Baird's efforts (Ripley 1971). Baird was the Institution's first curator and, starting in 1878, its second Secretary. Baird had a broad interest in natural history but is best known for his book *A History of North American Birds*, published in 1874, although his works on fishes were equally important. As the first U.S. Commissioner of Fisheries (starting in 1871) he did much to promote sound fisheries practices as well as to oversee the establishment of a marine biology laboratory at Woods Hole in Massachusetts (Rivinus & Youssef 1992).

[55] James Hall (1811–1898) was an early paleontologist in the United States (Clarke 1923). Educated at the Rensselaer Polytechnic Institute in Troy, New York, where one of his professors was Torrey's own early mentor, Amos Eaton. Hall's work with the New York survey, started in 1836, ultimately resulted in his appointment as the State's paleontologist. It was at this time, too, that Hall studied the stratigraphy of New York and established the modern nomenclatural practices for defining, naming, and classifying strata. After working in such states at Iowa and Wisconsin, he returned to New York in 1866 and became director of the New York State Museum of Natural History. Through Torrey, Hall was able to examine a multitude of fossils obtained on the various western North American expeditions. He was a founding member of the National Academy of Sciences and the first president of the Geological Society of America.

[56] Arthur Carl Victor Schott (1814–1875), German by birth, gathered plants not only on the Mexican Boundary Survey but also in Brazil, Colombia, and Mexico. On the Survey, Schott gathered not only plants and animals but drew many of the illustrations that went into Emory's report. Some of his most elegant illustrations were those of the Native Americans encountered in Texas and the Southwest (see Fig. 29, above).

[57] Charles Christopher Parry (1823–1890) would have a continuing role for much of the last three decades of Torrey's life. Born in England, his family moved to the United States in 1832 and settled in New York City where, in time, young Parry studied botany with Torrey in pursuit of a degree in medicine, which he received in 1846. He moved to Davenport, Iowa, in 1843, and in 1847 Parry became a member of a geological survey group for Iowa. He then accepted the position of botanist and surgeon on the United States and Mexican Boundary Survey, which lasted from 1849 until 1853. His experience on the Boundary Survey established Parry's reputation as a skilled botanist and because of his association with Torrey and Gray he was able to travel each summer almost yearly to collect plants in the West, especially in Colorado, Utah, and California. For three years (1869–1871) Parry was the first botanist for the U.S. Department of Agriculture to serve at the Smithsonian Institution. Numerous plants where named for Parry, and it was he who named Gray Peak and Torrey Peak in the Colorado Rocky Mountains for his

two botanical mentors. His 1883 paper on early botanical collections along the Pacific Ocean is most informative, although now somewhat dated. The primary source of information on Parry is a 1997 book by W.A. Weber.

[58] The bibliographic problems associated with the railroad reports have been discussed at length by Johnston (1943) and by McKelvey (1959). Most of the botanical reports were prepared by Torrey (1856, 1857a, b, c), Torrey and Gray (1857a, b), or, at the end, by Gray (1860) alone, with additional essays by others. John Milton Bigelow (1804–1878) was the surgeon-naturalist for the Amiel Weeks Whipple (1818–1863; Fig. 40) expedition in 1853 and 1854; Bigelow published two reports in 1857, with the cacti treated jointly by himself and Engelmann. John Strong Newberry (1822–1892), eventually the chair of the geology department at Columbia College (1866–1890), was also a friend of Torrey's. Both Torrey and Gray assisted Newberry in his 1857 report. William Starling Sullivant (1803–1873) concentrated on mosses and liverworts (Sullivant 1857), and Edward Tuckerman (1817–1886) contributed the lichens (Stafleu & Cowan 1986: 524). Elias Magliore Durand (1794–1873), a French botanist associated with the Academy of Natural Sciences of Philadelphia, and Theodore Charles Hilgard (1828–1875), a physician and friend of George Engelmann, described the plants obtained by Adolphus L. Heermann (1818–1865; Fig. 41) in California in 1853 during the Williamson expedition. Heermann, a noted birder (Stone 1907), is best known for his ornithological discoveries (Beidleman 2006). The final contributions to the railroad reports were published in 1860 by Gray and by James Graham Cooper (1830–1902). Cooper, a military surgeon and naturalist, was an assistant to Baird and saw that the plants of the Pacific Northwest were catalogued even though Cooper's major contribution was a two-volume work on ornithology published in 1870 with Baird (Coan 1983; Beidleman l.c.).

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Figure 40. *Hesperoyucca whipplei* (Torr.) Baker

[59] Joseph Christmas Ives (1829–1868), initially an assistant to Whipple on the railroad surveys, was along the Colorado River in 1857 and 1858. The geologist John Newberry, who was associated with the newly established Smithsonian Institution, served Ives as his surgeon/naturalist. The 1861 Ives report, with Gray and others, was one of Torrey's last contributions to the botany of a western expedition.

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Figure 41. *Eriogonum heermanni* Durand & Hilg. var. *sulcatum* (S. Watson) Munz & Reveal

[60] An online history of the Torrey Botanical Club is available online (Cooney 2000).

[61] Nathaniel Lord Britton (1859–1934) was a founder and the first director of the New York Botanical Garden established in 1891. Britton and his colleagues at the Garden believed that a major focus of their research should be floristics. As a result Britton authored or co-authored floras of the northeastern United States (1888, 1889, 1896–1898, 1901, 1905b, 1907b, 1913), the Bahama Islands (1905a, 1905c, 1906, 1907a, 1918a, 1920), and Porto Rico and the Virgin Islands (1918b, 1923–1924, 1925–1930). Britton also felt botanists at the Garden should conduct monographic studies, so it was that Joseph Nelson Rose (1862–1928) and Britton published monographs on Crassulaceae (1903) and Cactaceae (1919–1923). Addison Brown (1830–1913), president of the Garden and co-author with Britton of *An Illustrated Flora of the Northern United States, Canada and the British Possessions*, formulated common names for the species recognized in this work. The accompanying *Manual of the Flora of the Northern States and Canada*, published in 1901, was not only designed to promote Britton and Brown's three-volume illustrated flora but to compete directly with Gray's *Manual*, then authored by Sereno Watson (1826–1892), Gray's successor at Harvard University, and by John Merle Coulter (1851–1928), president of Lake Forest University. Coulter later moved to New York and was involved in the establishment of the Boyce Thompson Institute for Plant Research (Rodgers 1944). A seventh edition of Gray's *Manual* was published by Benjamin Lincoln Robinson (1864–1935) and

Merritt Lyndon Fernald (1873–1950) in 1908. Britton and Brown revised their illustrated flora in 1913. The final acts in this regional competition happened in the 1950s. After decades of labor on a new *Manual of Botany*, Fernald published his revision in 1950, the book appearing just three months before he died. New York responded with Henry Allan Gleason's (1882–1975) *The New Britton and Brown Illustrated Flora* in 1952; this was followed a decade later by Gleason and Cronquist's *Manual* in 1963 (revised in 1991) which was subsequently augmented by illustrations (Holmgren 1998). Gleason, known primarily as an ecologist (McIntosh 1975; Nicolson 1990; Nicolson & McIntosh 2002), came to the Garden in 1919 and in the 1930s moved into taxonomy and worked mainly in South America (Smith 1951; Cronquist 1976; see also his unpublished "The short and simple annals of Henry A. Gleason" in the Archives at the Garden) before concentrating on a new Britton and Brown flora.

[62] John Kunkel Small (1869–1938) became curator of Torrey's herbarium at Columbia College in 1895, but with the herbarium's transfer to the New York Botanical Garden in 1898, he began his 40-year career with the Garden (Barnhart 1935, 1938). A prolific author of some 450 published papers (see Stafleu and Cowan 1985: 650, for a sample) and a botanical collector of over 60,000 specimens, Small contributed significantly to the growth of the Garden. His work on Polygonaceae was monographic (Small 1895, 1898, 1906). He is best known for his flora of the southeastern United States (Small 1903, 1913, 1933). In 1918, the illustrator Mary Emily Eaton (1873–1961) traveled with him, and her efforts are preserved in the Library at the The Natural History Museum in London, the National Geographic Society, New York Botanical Garden, and the Smithsonian Institution (Mitich 2000). Small published a number of individual papers in 1925 and in 1927 on *Iris* in the journal *Adansonia*, with each species illustrated by a color plate; the originals art work is at the New York Botanical Garden (Small & Alexander 1931).

[63] For western botanists, Per Axel Rydberg (1860–1931) is synonymous with a period of proliferation of private journals, scientific names, and a power struggle to control systematic botany in the United States (Reveal 1991; Reveal & Pringle 1993; Tiehm & Stafleu 1990). Publication of new American plant names was controlled by Torrey until 1861, when the task fell to Gray. Watson and Robinson attempted to maintain dominance after Gray's death in 1888, but by then western rebels were wresting control of their own material. Prior to this, either all new plants went to Torrey and Gray to be named or they assigned others to name them. Thus, few new species were proposed during the period from 1830 until 1888 without the expressed approval of Torrey or Gray. For western botanists, now residing at a growing number of land grant colleges, the mere idea that Gray had to approve any new species before it could be published was an anathema. John Coulter assumed this role for papers published in the *Botanical Gazette* in 1875; Nathaniel Britton did the same for the *Bulletin of the Torrey Botanical Club* when he became editor. Authors were required to send specimens along with their papers, and only once the plants were deemed to be worthy of a name would these editors allow a paper be published. Floristic work was also controlled, albeit to a lesser degree, by the Smithsonian Institution.

Two early rebels were Edward Lee Greene (1843–1915), who began *Pittonia* in 1887, and Marcus Eugene Jones (1852–1934), who published *Contributions to Western Botany* starting in 1902 (Welsh 1982; Lenz 1986). Willis Linn Jepson (1867–1946) edited *Erythea* from 1893 until 1922. *Zoe*, a journal published in San Francisco by the Zoe Publishing Company starting in 1890, was the creation of Townshend Stith Brandegee (1843–1925) and his wife Mary Katherine [Lane, Curran] Brandegee (1844–1920). Even Rydberg attempted to control who and what was published, especially in the *Bulletin of the Torrey Botanical Club*, well into the 1920s.

Rydberg was a "splitter." His monographic and floristic efforts were considerable (Stafleu & Cowan 1983: 1014) during his tenure at the Garden (1906–1931). His most noteworthy were *Catalogue of a Flora of Montana* (1900), *Flora of Colorado* (1906), *Flora of the Rocky Mountains* (1917, 1923), and *Flora of the Prairies and Plains of Central North America* (1932). His monographic work on *Astragalus* and on Rosaceae were all published in the *Bulletin of the Torrey Botanical Club*.[64] Arthur John Cronquist (1919–1992) was one of the foremost

taxonomist of the twentieth century to be associated with the New York Botanical Garden in fulfilling Britton's mandate for monographic and floristic research (Barkley 1992, 1996; Ertter 1993; Takhtajan 1996). He came to the Garden in 1943 and remained until 1946 only to return in 1952. Over his last 40 years he was actively involved in floristics, first with Gleason, then with Charles Leo "Hitchy" Hitchcock (1902–1986) and Francis Marion Ownbey (1910–1974) on an illustrated flora for the Pacific Northwest (Hitchcock et al. 1955–1969; Hitchcock & Cronquist 1973) and finally the *Intermountain Flora*, an eight-volume work that was first published in 1972. Cronquist published treatments in six of the volumes (with one by Rupert Charles Barneby [1911–2000]). The last volume was completed in 2012 by Noel H. Holmgren, Patricia K. Holmgren (Fig. 42), and myself in collaboration with others. Globally, Cronquist is best known for his popular textbooks (1961, 1971, 1973, 1982), a work on plant geography with Gleason (1964), and most of all for his summaries on the classification of flowering plants (1968, 1981, 1988).

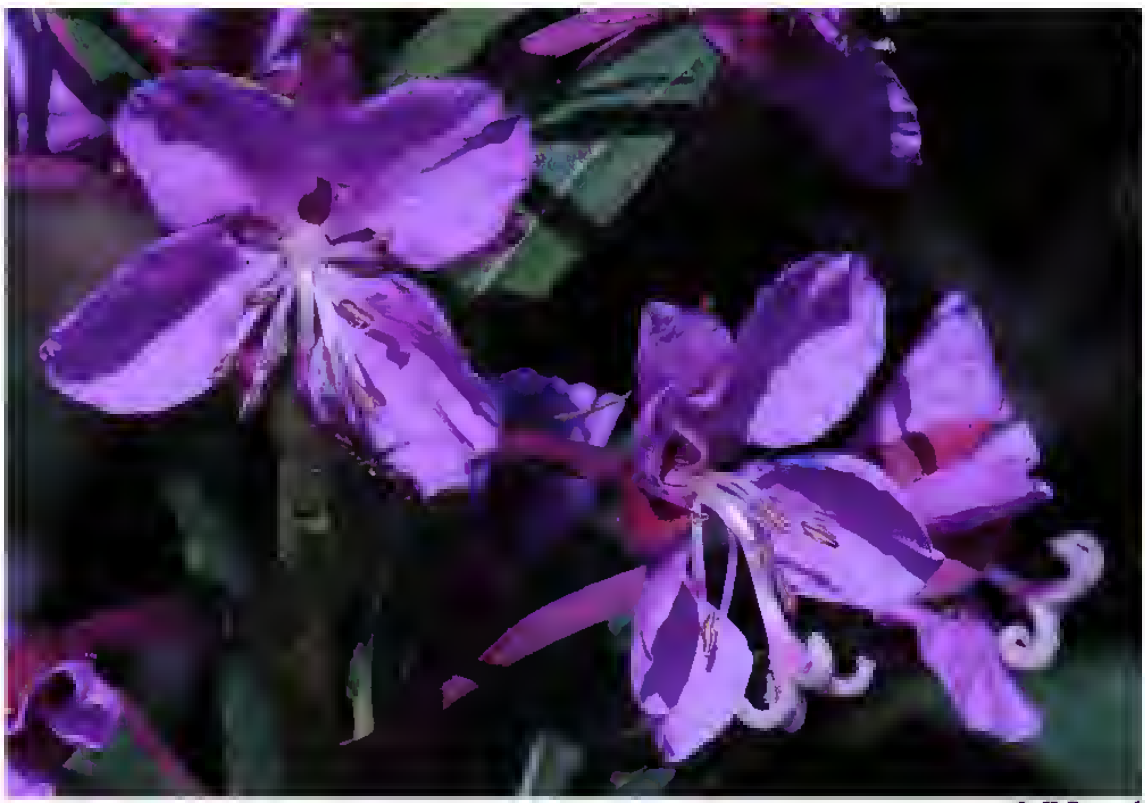

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Figure 42. *Chamerion angustifolium* (L.) Holub var. *canescens* (A.W. Wood) N.H. Holmgren & P.K. Holmgren

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Figure 43. *Ipomoea leptophylla* Torr.

The type of *Ipomoea leptophylla* was gathered by Frémont on 22 July 1842, most likely near present-day Glendo, Platte County, Wyoming. The above was photographed 170 years later (in 2012) along the Oregon Trail near Fort Laramie in Goshen County, Wyoming.

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BARCODING THE ASTERACEAE OF TENNESSEE, TRIBE COREOPSIDEAE

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ABSTRACT

Results from barcoding studies of tribe Coreopsideae for the Tennessee flora using the nuclear ribosomal ITS marker are presented and include the first complete reports for 2 of the 20 species of the tribe that occur in the state, as well as updated reports for several others. Sequence data from the ITS region separate most of the species of *Bidens* in Tennessee from one another, but species of *Coreopsis*, especially those of sect. *Coreopsis*, have ITS sequences that are identical (or nearly so) to at least one congener. Comparisons of sequence data to GenBank records are complicated by apparent inaccuracies of older sequences as well as potentially misidentified samples. Broad survey of *C. lanceolata* from across its range showed little variability, but the ITS sequence of a morphologically distinct sample from a Florida limestone glade area was distinct in lacking a length polymorphism that was present in other samples.

Tribe Coreopsideae is part of the Heliantheae alliance and earlier was often included in an expanded Heliantheae (Anderberg et al. 2007) in which it was usually treated as a subtribe (Crawford et al. 2009). The tribe shows a small burst of diversity in the southeastern USA involving *Bidens* and *Coreopsis* sect. *Coreopsis*. The current study continues the effort to characterize the levels and patterns of molecular diversity found in species of Asteraceae in Tennessee and southeastern North America (Schilling & Floden 2012, 2014; Schilling 2013) and to assess the potential of the nuclear ribosomal ITS region as a molecular barcode to identify species.

Coreopsideae in Tennessee includes three genera and about 20 species (Chester et al. 2009). The two species of *Cosmos* have been collected as garden escapes and may be adventive in disturbed sites. *Bidens* and *Coreopsis* have up to nine species each, all of which may be native, although this is not certain for some, particularly of *Coreopsis*, which are popular garden plants. The generic limits and separation of *Bidens* and *Coreopsis* continue to be problematic (Crawford et al. 2009). Two species of *Coreopsis*, *C. delphinitfolia* and *C. latifolia*, are considered to be rare both globally and in the state (Crabtree 2012).

The goal of this study was to conduct a survey of variation for the ITS marker for all species of Coreopsideae that occur in Tennessee. Particular emphasis was placed on *Coreopsis* and *Bidens*, both of which include modest radiations in southeastern North America and for which species boundaries are still under discussion. Within *Coreopsis*, a broader regional sampling of *C. lanceolata* was undertaken to help evaluate whether a morphologically distinct entity that occurs in limestone glade habitats in Florida (Johnson et al. 2013) is also distinct at the molecular level. Also included were several samples of horticultural cultivars that might be encountered as escapes.

Materials and methods

DNA was extracted from leaf samples either collected fresh or taken from herbarium specimens (Table 1). DNA extraction, PCR amplification, and sequencing protocols followed Schilling and Floden (2011). Samples that had length polymorphisms in the ITS region were sequenced with multiple primers. GenBank accession numbers are provided in Table 1. Although

this study was not designed to undertake a rigorous phylogenetic analysis, a maximum likelihood tree was generated using MEGA 6 (Tamura et al. 2013) to provide a convenient way to make a comparative visualization of the sequence results. The tree was rooted using a sample of *Gaillardia* (Heleniеae), another member of the Heliantheae alliance. The analysis also utilized sequences deposited at GenBank of conspecific samples or closely related species of Coreopsideae.

Table 1 Plant material used for ITS barcoding studies of Coreopsideae. All voucher specimens at TENN.

Species	DNA#	Genbank	Voucher info
BIDENS L.			
B. aristosa Britton	2544	KM347897	*Schilling 07-DNA2544*, Knox Co., TN
B. aristosa Britton	3817	KM347898	*Floden 1707*, Campbell Co., TN
B. bipinnata L.	3818	KM347899	*Estes and Beck 6410*, Fentress Co., TN
B. bipinnata L.	3530	KM347900	*DeSelm 02-219*, Bradley Co., TN
B. cernua L.	3819	KM347901	*Floden 1415*, Campbell Co., TN
B. cernua L.	3531	KM347902	*Webb 6912*, Benton Co., TN
B. discoidea Britton	3532	KM347903	*Webb 6911*, Benton Co., TN
B. discoidea Britton	3820	KM347904	*DeSelm 02-287*, Claiborne Co., TN
B frondosa L.	3533	KM347905	*Webb 7628*, Henry Co., TN
B frondosa L.	3821	KM347906	*Estes and Beck 8402*, Grundy Co., TN
B frondosa L.	2624	KM347907	*Schilling 7-BC2624*, Knox Co., TN
B. polylepis S.F. Blake	3822	KM347908	*Souza 86-609*, Dickson Co., TN
B. polylepis S.F. Blake	2588	KM347909	*Schilling 07-DNA2588*, Knox Co., TN
B. tripartita L.	3823	KM347910	*Webb 6910*, Benton Co., TN
COREOPSIS L.			
C. auriculata L.	3016	KM347910	*Schilling 10-DNA3016*, Campbell Co., TN
C. basalis S.F. Blake	3816	KM347913	*Schilling 13-DNA3816*, cv. Sunburst
C. delphiniifolia Scherff	3091	KM347914	*Wofford and Clebsch 91-19*, Polk Co., TN
C. sp. nov. –Florida Glades	3622	KM347915	*Johnson 13*, Jackson Co., FL
C. grandiflora Hogg ex Sweet	3092	KM347916	*DeSelm s.n. 5/14/06*, Bradley Co., TN
C. grandiflora Hogg ex Sweet	3826	KM347917	*Estes and Beck 7618*, Marion Co., TN
C. grandiflora Hogg ex Sweet	3815	KM347918	*Schilling 13-DNA3815*, Greenhouse plant
C. grandiflora var. *inclinata* J.R.Allison	3679	KM347919	*Allison 12086*, Bibb Co., AL
C. lanceolata L.	3093	KM347920	*McCoy s.n. 5/30/07*, Rutherford Co., TN
C. lanceolata L.	3621	KM347921	*Johnson 13*, Gadsden Co., FL
C. lanceolata var. *villosa* Michx.	3650	KM347922	*Schmidt97-132*, Mackinac Co., MI
C. lanceolata L.	3651	KM347923	*Stutts 351*, Muscogee Co., GA
C. lanceolata L.	3652	KM347924	*Thomas 88326*, Webster Par., LA
C. lanceolata L.	3653	KM347925	*Thomas 159401*, Nevada Co., AR
C. lanceolata L.	3863	KM347926	*DeSelm s.n.2000*, Monroe Co., TN
C. lanceolata L.	3867	KM347927	*R. Kral 1983*, Warren Co., TN
C. lanceolata L.	3886	KM347928	*Bailey s.n.*, Perry Co., TN
C. lanceolata L.	3868	KM347929	*R. Kral 385*, 1975, Sumner Co., TN
C. lanceolata L. cv. Sterntaler	3813	KM347930	*Schilling 13-DNA3813*, Garden plant
C. lanceolata L. cv. Sunfire	3814	KM347931	*Schilling 13-DNA3814*, Garden plant
C. lanceolata L.	3827	KM347932	*Souza 88-164*, Dickson Co., TN
C. lanceolata var. *villosa* Michx.	3649	KM347933	*Godfrey 55430*, Calhoun Co., FL
C. lanceolata var. *villosa* Michx.	3864	KM347934	*Rhinehart s.n. 2001*, Sequatchie Co., TN
C. lanceolata var. *villosa* Michx.	3865	KM347935	*Mcneilus 00-460*, Polk Co., TN
C. lanceolata var. *villosa* Michx.	3866	KM347936	*McCoy s.n. 5/30/07*, Rutherford Co., TN
C. lanceolata var. *villosa* Michx.	3869	KM347937	*R.Kral 385, 1975*, Sumner Co., TN
C. latifolia Michx.	3094	KM347938	*Murrell* et al *948a*, Polk Co., TN
C. latifolia Michx.	3828	KM347939	*Patrick* et al *4978*, Polk Co., TN

C. major Walt.	2567	KM347940	*Schilling 07-DNA2567*, Unicoi Co., TN
C. major Walt.	3837	KM347941	*Schilling 2013-02*, Campbell Co., TN
C. pubescens Ell.	3095	KM347942	*Estes 9327*, Morgan Co., TN
C. pubescens Ell.	3830	KM347943	*Estes* et al *9326*, Cumberland Co., TN
C. rosea Nutt.	3838	KM347944	UT Garden 6/21/2013, Garden plant
C. tinctoria Nutt.	3831	KM347945	*Estes 4897*, Giles Co., TN
C. tinctoria Nutt.	3839	KM347946	UT Garden 6/21/2013, Garden plant
C. tripteris L.	3525	KM347947	*Floden 1719*, Campbell Co., TN
C. tripteris L.	3832	KM347948	*Estes and Beck 8481*, Bledsoe Co., TN
COSMOS Blume			
C. bipinnatus Cav.	3851	KM347948	*Schilling 2013-04*, Knox Co., TN
C. sulphureus Cav.	3870	KM347949	*Schilling 2013-06*, Knox Co., TN

Results and discussion

The newly obtained ITS sequences for Coreopsideae ranged in length from 631-640 bp. Sequences of *Coreopsis* were 631-640 bp in length; of *Bidens* were 635-639 bp, and of *Cosmos* were 638-639 bp. Many of the sequences from samples of *Coreopsis*, and some of *Bidens*, had polymorphisms. The ITS sequences for a subset of sect. *Coreopsis* species (*C. grandiflora*, all but one sample of *C. lanceolata*, and *C. pubescens*) all showed evidence of a length polymorphism involving a poly-G region at position 498-503 in the aligned matrix; the inferred lengths of the poly-G region for these samples were 5 and 6 bp. All other species of *Coreopsis* had a poly-G of 4 or 5 bp in length for this region, except for the sample representing a possible new taxon from limestone glades in Florida that had a poly-G region of 6 bp in length at this position. There were also length polymorphisms at different positions in the samples of *C. auriculata*, *C. major*, and *C. tinctoria*. Many samples of *Coreopsis* also had numerous positional polymorphisms (e.g., detected by the presence of a double peak; also called SNAPs, Whittall et al. 2000). The ITS sequences for some samples of *Bidens* also showed evidence of polymorphisms. Sequences of all samples of *B. discoidea* and *B. frondosa* shared a common suite of numerous positional polymorphisms and a length polymorphism. In contrast, samples of *B. aristosa* and *B. polylepis* had ITS sequences that were identical to one another and contained only three positional polymorphisms and no length polymorphisms. Sequences of the samples of *B. bipinnata*, *B. cernua*, and *B. tripartita* almost completely lacked any polymorphisms.

Many of the species of Coreopsideae from Tennessee were not well separated from close congeners based on ITS sequence results (Fig. 1). Within *Coreopsis*, there was little differentiation among numerous samples of sect. *Coreopsis*, including *C. auriculata*, *C. basalis*, *C. grandiflora*, *C. lanceolata* (both var. *lanceolata* and var. *villosa*), and *C. pubescens*; any differences involved whether or not there was a polymorphism at a given position. The separation of some samples of the section drawn from GenBank records (*C. auriculata* AY553677/ AY553678; *C. basalis* AY553705/ AY553706; *C. grandiflora* AY553707/ AY553708) seem likely to reflect errors in sequence reads rather than real differences, and these are relatively old records dating from when ITS1 and ITS2 were sequenced individually. An undetected length polymorphism could easily give rise to inaccurate base calls in the downstream sequence. A GenBank sample (GU724273) labeled *C. tinctoria* placed within this clade seems likely to be a misidentification. There was also little differentiation of our samples of *C. delphinitifolia* and *C. major*, although the GenBank samples labeled for each of these species were different (it appears that the GenBank sample for *C. major* might be misidentified and actually represent a *C. tripteris*). *Coreopsis delphinitifolia* has been proposed to be an allopolyploid involving *C. major*, *C. tripteris*, and *C. verticillata* L. (Smith 1976), but there was no evidence in the sequence or pattern of polymorphisms of either of the latter two species. A series of clones of a sample of *C. verticillata* deposited at GenBank (labeled there as *Coreopsis* sp. 1154; identified by the collector as *C. verticillata*, M. Vincent pers. comm.) showed some variability, but the variants appear

to represent autapomorphic changes. Within *Bidens*, there was greater differentiation among most but not all species. The exceptions involved *B. aristosa* and *B. polylepis*, which had identical sequences, and *B. discoidea* and *B. frondosa*, for which the ITS sequences were essentially identical. Both of these appear to be closely related (or perhaps not completely differentiated) pairs of species. For Coreopsideae and particularly for *Coreopsis*, these results suggest that although the ITS marker can narrow the possibilities for species level identification, it does not provide a suitable marker to distinguish uniquely several of the species.

Figure 1. Maximum likelihood bootstrap tree (500 replicates) showing relationships of species of Coreopsideae based on ITS sequence data, using *Gaillardia pulchella* (Heleniеae) as the outgroup. Newly obtained sequences designated by DNA number preceding species name (Table 1), GenBank numbers for other sequences follow species name. * = sample from Tennessee.

The low level of differentiation for the ITS marker at the species level within *Coreopsis* sect. *Coreopsis* complicates assessment of the potential distinctiveness of material from limestone glade habitats in Florida that is distinct morphologically from *Coreopsis lanceolata* (Johnson et al. 2013). There was, however, one clear difference between the Florida glade sample and the samples of *C. lanceolata* in the lack of any evidence in the former of a length polymorphism for the poly-G region that is almost universally present in other samples of not only *C. lanceolata* but also of *C. grandiflora* and *C. pubescens*. In addition, the Florida glade sample also exhibited a positional polymorphism at position 231 (A/G=R) that was instead present as an unambiguous G in all samples of *C. lanceolata*. By contrast, the sample of *C. grandiflora* var. *inclinata* from the Ketona Glades in Bibb Co., Alabama, had an ITS sequence that was identical to that of other samples of *C. grandiflora*. Thus even the small differences in ITS sequence in the Florida limestone glade sample appear to characterize it as distinctive, given the overall uniformity of the group for this marker.

The potential usefulness, but also the limitations, of utilizing the ITS region as part of a universal barcode can be seen in the results of this study. The ITS region remains popular for molecular systematics studies (e.g. Wang et al. 2014), in part because it is easily obtained even from herbarium material, as was the case here. All of the herbarium specimens that were extracted provided results, including one almost 40 years old. The ITS sequence data would allow near, if not exact, placement of all of the samples. However, the length polymorphisms, which were present in many of the samples of *Coreopsis* and also in some of *Bidens*, would complicate easy interpretation of results from direct sequencing. The database represented by GenBank samples continues to be problematic, both because of apparent misidentifications of material and also because of low quality of some older sequences. Nevertheless, as a quick and straightforward approach, surveying the ITS region as part of an initial analysis of species diversity appears to be a useful tool.

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GRINDELIA OXYLEPIS (ASTERACEAE, ASTEREAE) NEW TO NEW MEXICO

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ABSTRACT

A large population of *Grindelia oxylepis* is reported from 2.6 km north of the Mexican border in southwestern Doña Ana Co., New Mexico. Plants occurred in a playa that apparently held water several times in 2014. This is the first report for this otherwise Mexican species in New Mexico and the second report for its occurrence in the USA. The species was first collected in the USA in 1946 in Presidio Co., Texas. If varieties are recognized in *G. oxylepis*, the New Mexico record represents the var. *oxylepis*. Plants are up to 1 m tall, taller than reported in the literature, and have leaves similar to plants from northern Chihuahua.

Recently while I was traveling within a few kilometers of the Mexican border on the "Border Highway" (Doña County Rd A003, a continuation of NM Highway 9 from the Luna County border eastward) I noticed a large population of a robust species of *Grindelia* that I did not recognize. This population occupied an estimated four hectares in the southwestern portion of a playa (a regional term for a shallow, temporary lake with a level or nearly level bottom) situated next to and north of the

Figure 1. The playa in southwestern Doña Ana Co., New Mexico, along north side of the "border highway," where *Grindelia oxylepis* was discovered. Brownish plants at margin of playa and plants in the water are *G. oxylepis*. Photo taken 24 September 2014, several days after heavy rain. Plants are now mostly in fruit. Dense, green plants in foreground are *Laennecia coulteri*.

road. The construction of the raised road across this playa about two decades ago now prevents precipitation runoff from the surrounding low desert hills to disperse across the larger portion of the playa to the south, as it probably did in the past. In the southwestern corner of the portion of the playa north of the highway water collects and stands for some time after significant rain (Fig. 1), as it apparently did several times in the late summer of 2014. This playa is readily apparent in Google Earth by entering the geographic coordinates given in the specimen citation below. The plants were identified as *Grindelia oxylepis* Greene, the first record for the species in New Mexico and apparently the second record for the USA.

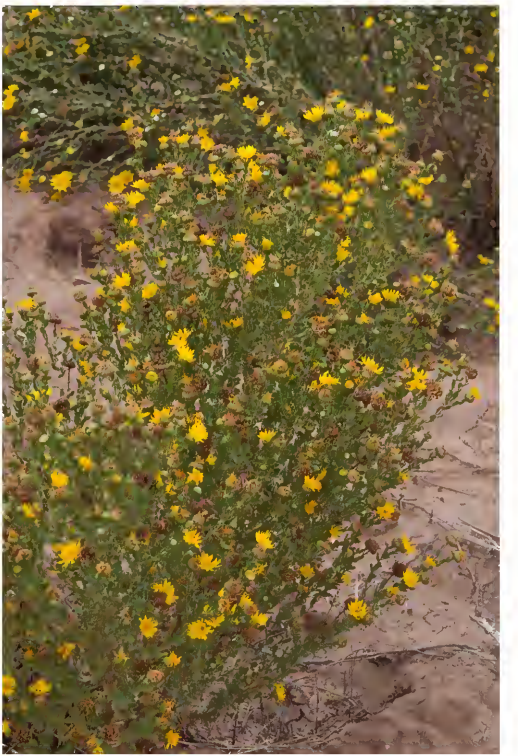

Figure 2. A plant of *Grindelia oxylepis* at edge of playa, showing extensive branching. Photo taken 14 September 2014, at the time of collection. Plant is 1 m tall.

Figure 3. *Grindelia oxylepis* from Doña Ana Co., New Mexico. (Left) Flower head, showing straight or slightly spreading phyllaries subtended by a leaf with callus-tipped teeth; photo taken 14 September 2014. (Right) Cypselae from heads collected on 24 September 2014; bristle-like pappi have been dropped; scale at edge of photo is in millimeter increments.

Voucher. **USA. New Mexico.** Doña Ana Co.: Doña Co. Rd A003 (an easterly continuation of NM Hwy 9) between mile markers 121 and 122, 41.5 km W of terminus of hwy in Santa Teresa, 20 km E of Luna Co. line, 2.6 km N of the Mexican border, N side of hwy, 31° 48.374' N, 107° 06.160' W, in moist silt in and at edge of playa, with *Psilactis asteroides, Laennecia coulteri, Prosopis, Atriplex* around edge of playa, the *Grindelia* the most common species within playa, elev. 1235 m, 14 Sep 2014, *R. Spellenberg 14971* (NMC).

The New Mexico plants of *Grindelia oxylepis* are annual in duration and completely glabrous, as characteristic of the species, and leaf lobes are tipped by a small spinulose callus (Fig. 3), as characteristic of the species in northern Chihuahua (Nesom 1990, who suggested that this might reflect introgression with the the spinulose-tipped *G. arizonica*) — elsewhere over the range of *G. oxylepis*, the lobe tips are blunt and glandular-resinous. Plants are up to about 1 m tall, notably taller than the range given in either Henrickson (1997) or Strother and Wetter (2006), who noted, respectively, that plants may be up to 70 cm and 55 cm tall, and they are repeatedly branching from the base and distally (Fig. 2), in contrast to the observation by Nesom that they usually are single-stemmed from the base. Heads are hemispherical (Fig. 3) and more or less depressed upon drying. The cypselae (Fig. 3) are distinctively "blocky" and prominently rugose, readily dropping their 2-3 awns.

Mexican Gumweed (vernacular name from USDA website <http//plants usda.gov/>) is widespread in Mexico, occurring from northern Chihuahua (about 90 km south of the USA border) to south-central Durango and central San Luis Potosí (as mapped by Nesom 1990), growing in moist, low, often disturbed areas (Henrickson & Johnston 1997). Nesom shows one location in Presidio Co., Texas, based upon a collection made on 9/25/1946 (*J.H. Russell 2087*, LL). No other USA collections appear on the University of Texas herbarium website (<http //www biosci utexas edu/prc/Tex html>). The USDA website also shows the species to be "native, [but with] no county data" in Arizona; no documenting specimens for Arizona were located in the herbaria database SEINET (<http //swbiodiversity org/ seinet/index php>). Thus, *Grindelia oxylepis* is documented for the second time nearly 70 years after its initial discovery in the USA by the collection from southern New Mexico, at the northernmost point in its known range, where it occurs in a population consisting of many hundreds of individuals.

The taxon represented in New Mexico would be *Grindelia oxylepis* Greene var. *oxylepis* in a classification followed by Henrickson and Johnston (1997). Steyermark (1934) erected the var. *eligulata* Steyerm. as a rayless variety within *G. oxylepis* that occurs from southern Chihuahua to southern Coahuila and adjacent Nuevo Leon, not reaching the USA. Nesom (1990) elevated that variety to species level as *G. eligulata* (Steyerm.) Nesom. In their treatment for Flora of North America, Strother and Wetter (2006) described only radiate heads in *G. oxylepis* and made no mention of alternative classifications of taxa in this complex. The name *G. oxylepis* does not appear in the Manual of Vascular Plants of Texas (Correll & Johnston 1970).

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NEW AND NOTEWORTHY VASCULAR PLANT RECORDS FROM ALABAMA

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ABSTRACT

Seven species of vascular plants are documented as new to the native and naturalized flora of Alabama: *Ageratum houstonianum, Chlorophytum comosum, Exochorda racemosa, Euphorbia graminea, Hosta ventricosa, Phyllanthus evanescens,* and *Tithonia rotundifolia*. Complete sets of the specimens are housed at TROY, UWAL, and VDB. Records were determined using the Alabama Plant Atlas (Alabama Plant Atlas Committee 2014), the North American Plant Atlas (BONAP 2013), and other pertinent literature.

New records of vascular plants have accumulated for Alabama as a result of field studies. Six of the species reported represent non-native species established (at least locally) in the flora. The seventh species is possibly native to the state — *Phyllanthus evanescens* is a weedy taxon that may have been overlooked by previous collectors. It occurs in an area with other disjunct western species.

AGERATUM HOUSTONIANUM Mill. (Asteraceae)

Alabama. Montgomery Co.: Montgomery, Federal Drive at Alabama State Farmer's Market adjacent to Garrett Coliseum, weeds around parking lot, full sun, 32.405528° -86.267333°, 3 Nov 2013, *Diamond 24687*.

Native to Mexico and portions of Central America, *Ageratum houstonianum* has a long history of cultivation and establishment as a weed in many areas of the world (Johnson 1971). This species was not included in the Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011) nor has it been included on the Alabama Plant Atlas website (Alabama Plant Atlas Committee 2014). It has previously been reported for Alabama but there seems to be some confusion on this report.

Mohr (1901) reported *Ageratum conyzoides* L., listing *Ageratum mexicanum* Sims in synonymy, and noted this: the species is "escaped from cultivation. Waste and cultivated places near dwellings. Mobile County. Flowers lilac; July to October. Becoming a troublesome weed in the gardens." The original description of *A. houstonianum* was based on a specimen collected by William Houston in Mexico. Seeds were sent to Europe and the plant soon became a weed in greenhouses. The original description of *A. mexicanum* was based on plants grown from seed sent from Mexico, and Johnson (1971) states there is no question that this species is identical to *Ageratum houstonianum*. de Candolle later reduced *A. mexicanum* to one of four varieties of *Ageratum conyzoides*. Johnson (1971) treated Mohr's plant as *Ageratum houstonianum*, placing a dot on the distribution map for Mobile, Alabama. However in his discussion he stated that the "report of establishment in Alabama is probably based on errors in identification." Johnson did not list any specimens of *A. houstonianum* or *A. conyzoides* that he examined from Alabama.

The majority of Mohr's specimens are located at The University of Alabama Herbarium (UNA) and the United States National Herbarium (US). The University of Alabama has a single sheet of *Ageratum* collected by Mohr. The label bears Mohr's determination as *Ageratum conyzoides*. This identification was confirmed by M. Guzman in 1983. Steve Ginzbarg, Collections Manager at

UNA, examined the specimen at my request — he notes that the specimen lacks glandular hairs on the peduncles and phyllaries and keys to *A. conyzoides* in Cronquist (1980), Weakley (2012), and the Flora of North America North of Mexico treatment for *Ageratum* (Nesom 2006) (Ginzbarg, pers. comm.). Since previous reports of *A. houstonianum* from Alabama have cited either Mohr or Johnson, and since Mohr's specimen is clearly *A. conyzoides*, *Diamond 24687* apparently represents the first documentation of *Ageratum houstonianum* in Alabama (Figs. 1, 2).

CHLOROPHYTUM COMOSUM (Thunb.) Jacques (Agavaceae)

Alabama. Conecuh Co.: Evergreen, along a small creek in wooded area S of US Hwy 31, west of Bowles Street, and E of Park Street, W of old Evergreen Cemetery, 31.434910° -86.950095°, 22 Jun 2013, *Diamond 24273*.

A native of southern Africa, *Chlorophytum comosum* has been reported as naturalized in Australia and the United States (The University of Queensland 2011; USDA, NRCS 2013). Known by the common names "Spider Plant" or "Airplane Plant", it is one of the most popular cultivated plants in the world (Mucina and Rutherford 2006). This represents the first report of this taxon from Alabama. It was not included in the Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011), nor has it been included on the Alabama Plant Atlas website (Alabama Plant Atlas Committee 2014). This species has previously been reported from Hillsborough and Indian River counties in Florida (Wunderlin & Hansen 2008) and Lowndes County in Georgia (BONAP 2013). The plants were growing in a disturbed woodland adjacent to a small stream. Plants were observed to persist over several winters, dying back to ground level with freezing temperatures. Flowering was observed but no fruit were seen. Reproduction appears to be by plantlets produced on the inflorescence.

EXOCHORDA RACEMOSA (Lindl.) Rehd. (Rosaceae)

Alabama. Conecuh Co.: County Hwy 107, 0.06 mi NW of the Covington County line, overgrown lot adjacent to a closed gas station, with *Pyrus calleryana*, *Triadica sebifera*, *Prunus carolinian*a, and *Ligustrum sinense*, 31.505461° -86.701802°, 20 Mar 2014, *Diamond 24892*.

This represents the first report of this taxon from Alabama. It was not included in the Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011), nor has it been included on the Alabama Plant Atlas website (Alabama Plant Atlas Committee 2014). Widely cultivated, this native of China has escaped in several eastern and southern states of the USA (Invasive Plant Atlas of the United States 2014). It was first reported for South Carolina by Hill and Horn (1997). The plants at this site seem to be reproducing through root sprouts rather than by seed, as was speculated by Hill and Horn (1997) for the population in South Carolina. Seed capsules were observed but all "seedling" sized plants were connected to roots from larger plants.

EUPHORBIA GRAMINEA Jacq. (Euphorbiaceae)

Alabama. Conecuh Co.: Evergreen, Cooper Street, ca. 70 feet W of U.S. Hwy 31, growing in roadside gutter and in cracks in the side walk, 31.432966° -86.956310°, 16 Nov 2013, *Diamond 24693*. Montgomery Co.: Montgomery, Federal Drive at Alabama State Farmer's Marker adjacent to Garrett Coliseum, weeds around parking lot, full sun, 32.405528° -86.267333°, 3 Nov 2013, *Diamond 24686*.

This species is native from Mexico to northern South America (Webster & Bruch 1967). First collected in the USA from Florida in 1993 (Herndon 1994), it has now been reported from several additional Florida counties including two that are adjacent to Alabama (Wunderlin & Hansen 2008). It has also been reported from Arkansas and Texas (BONAP 2013). These collections represent the first reports of this taxon from Alabama. It was not included in the Annotated Checklist of the

Vascular Plants of Alabama (Kral et al. 2011). Although it has been included on the Alabama Plant Atlas website (Alabama Plant Atlas Committee 2014), no collections are represented. Vincent (2013) reported this species as new for the Bahamas and stated that it was collected "from disturbed sites where horticultural plants had recently been introduced from Florida nurseries." Both Alabama collections were from areas near where ornamental plants were being sold. The plants produce large numbers of seed and have persisted at the sites.

HOSTA VENTRICOSA (Salisb.) Stearn (Agavaceae)

Alabama. Coosa Co.: Intersection of Coosa County Hwy 40 and 0.28 mi E of U.S. Hwy 231, hardwood forest edge, with Hunter Hill, 32.837198° -86.223031°, 27 Jun 2013, *Diamond 24303*.

A native of China, this species is widely planted as an ornamental (Weakley 2012). It has previously been reported as an escape from several northeastern states and as far south as Kentucky and North Carolina (BONAP 2013). This represents the first report of this taxon from Alabama. It was not included in the Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011), nor has it been included on the Alabama Plant Atlas website (Alabama Plant Atlas Committee 2014).

TITHONIA ROTUNDIFOLIA (Mill.) S.F. Blake (Asteraceae)

Alabama. Crenshaw Co.: County Hwy 37, 1.85 mi N of Alabama Hwy 106, disturbed roadside in full sun, several plants over 6 ft tall, 31.616154° -86.347875°, 14 Nov 2012, *Diamond 23558*.

A native of Mexico and Central America, *Tithonia rotundifolia* is widely cultivated in warm climates and may persist (La Duke 2006). Previous reports of this species as naturalized in the USA are from Florida, Louisiana, and Texas (La Duke 2006; BONAP 2013). This represents the first report of this taxon from Alabama. It was not included in the Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011), nor has it been included on the Alabama Plant Atlas website (Alabama Plant Atlas Committee 2014). The species was collected on a disturbed roadside and was in early flower at the time of the first killing frost. Apparently some of the plants were able to produced seed and it has persisted at the site.

PHYLLANTHUS EVANESCENS Brandeg. (Phyllanthaceae)

Alabama. Macon Co.: County Hwy 1, 0.54 mi N of Macon County Hwy 23, Blackbelt roadside along a pasture fence, 32.240833° -85.795361°, 5 Oct 2012, *Diamond 23492*.

This represents the first report of this taxon from Alabama. It was not included in the Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011), nor was it reported from Alabama by Webster (1970), Weakley (2012), or BONAP (2013). Weakley reports the species from St. Charles Parish in Louisiana west to Texas and south into Mexico and Central America. The North American Plant Atlas maps the occurrence of this species in Arkansas, Louisiana, and Texas. Three other species with primarily western distributions have been collected as disjuncts in this or adjacent counties in the Blackbelt prairie — *Scutellaria drummondii*, *Atrema americanum*, and *Calylophus berlandieri*. This species was growing on a roadside near a cow pasture and it is possible that it could have been introduced. However, it was also growing with typical prairie species such as *Agaltnis heterophylla*, *Heliotropum tenellum*, *Ratibida pinnata*, and *Glandularia bipinnatifida*. It is equally as plausible to view this population as another native disjunct prairie species. This species is similar in appearance to the widespread *Phyllanthus caroliniensis*. *Phyllanthus evanescens* has winged stems, connate filaments, larger seed, and occurs in dry habitats on prairie clay soils (Webster 1970). Botanists working in the Blackbelt prairie region of Alabama and Mississippi should be on the lookout for this species.

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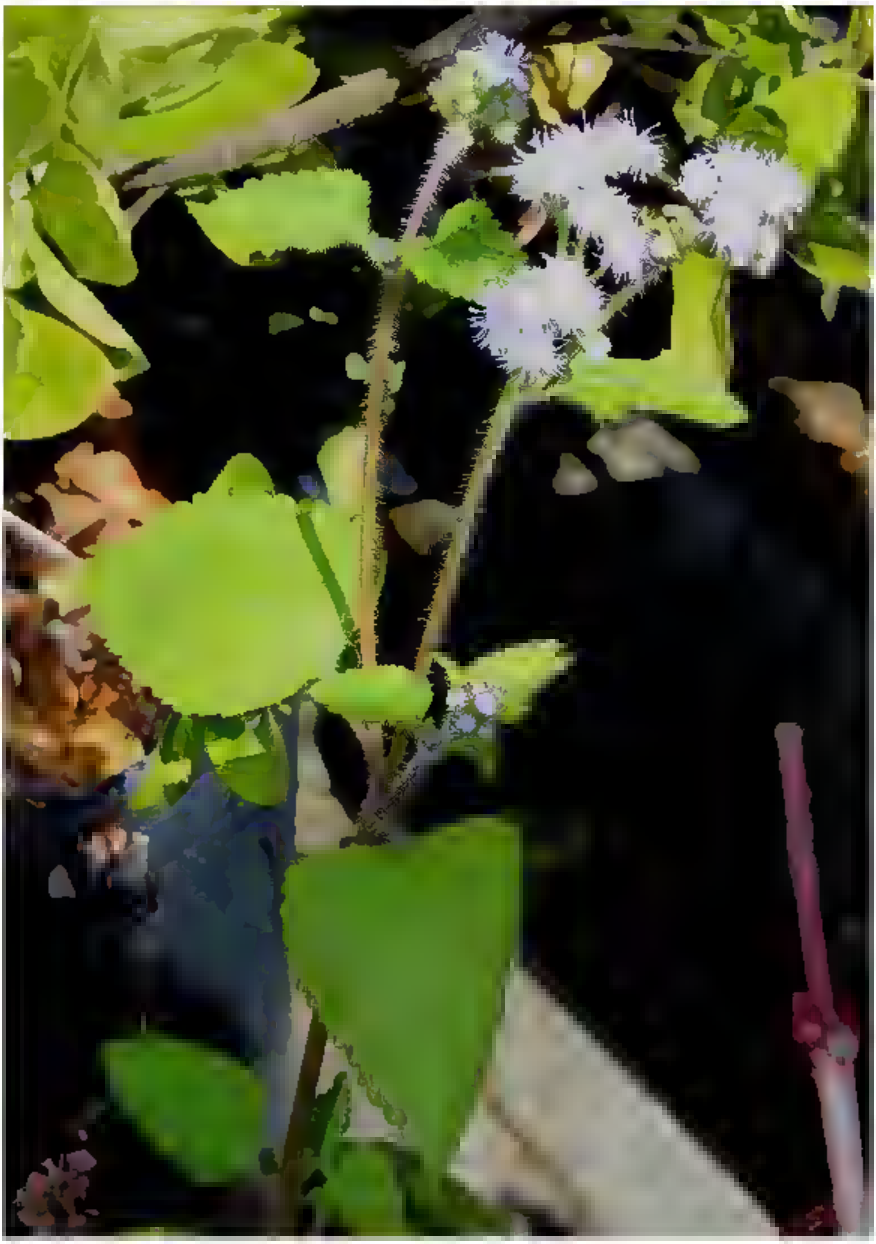

Figure 1 *Ageratum houstonianum*, general aspect of the plant

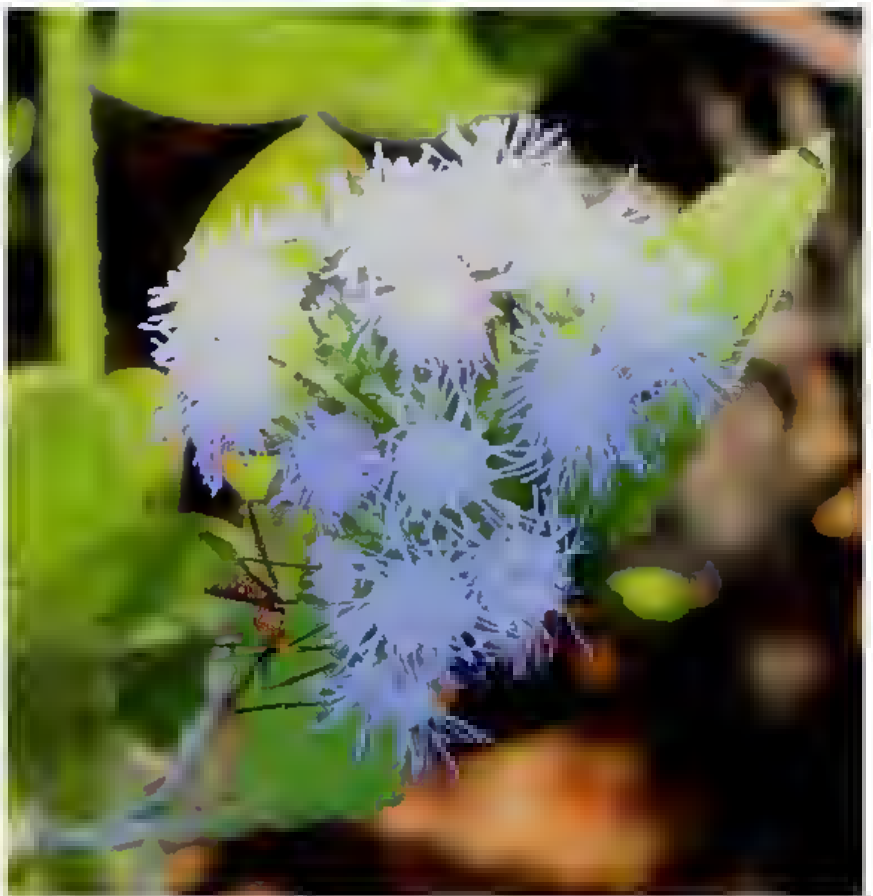

Figure 2 *Ageratum houstonianum* in flower

Figure 3 *Chlorophytum comosum* growing along a small stream

Figure 4 *Chlorophytum comosum* with vegetative plantlet

Figure 5 *Exochorda racemosa* in flower

Figure 6 *Euphorbia grammea* growing along the base of a building in Montgomery Alabama

Figure 7 *Hosta ventricosa* with fruit.

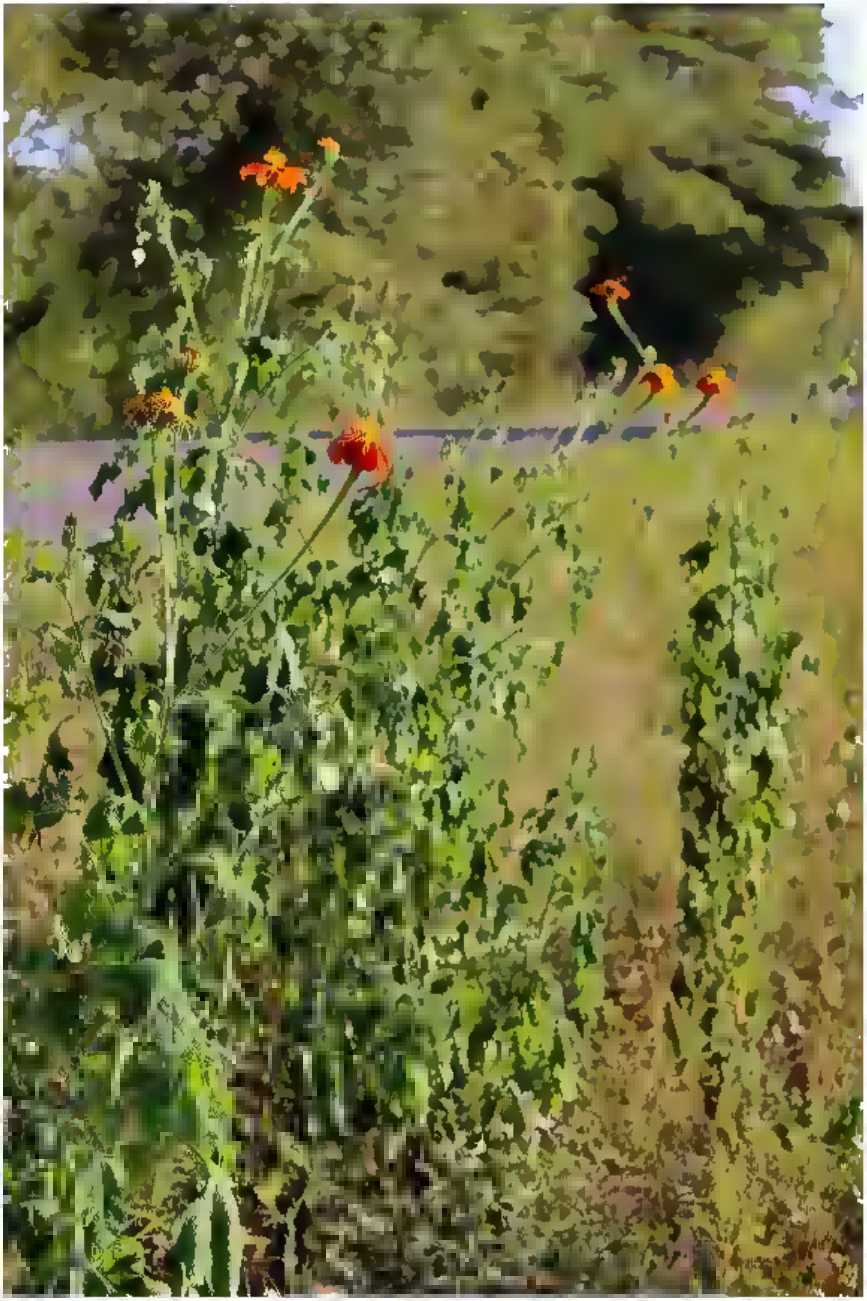

Figure 8 *Tithonia rotundifolia* growing on the roadside in Crenshaw County Alabama

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REVIEW OF PLANT ELEVATION CHANGES IN ARIZONA

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ABSTRACT

A recent paper (Brusca et al. 2013a) reported dramatic elevation range changes for 27 plant species in the Catalina Mountains of Arizona in the 50-year interval following Robert Whittaker and William Niering's vegetation studies in the early 1960s. Brusca et al. interpreted these differences as responses to climate change, but while the observations by Brusca et al. are consistent with what might be expected with a changing climate, correlation does not imply causation. Detecting significant change requires accurate knowledge not only of the actual ranges of species but also of species abundance and distribution, at two points in time. Determining the causes of any changes identified requires knowledge of population dynamics and of ecological processes occurring during the time period studied. The commentary here reviews the purported changes in Catalina species as well as other pertinent literature by addressing three main questions: What are the actual ranges of species analyzed? How do we detect changes in them? How can we determine the cause of any changes?

Increased warming, drought, and reduced stream flows are among recent ecological changes in the southwestern United States consistent with climate change. Garfin et al. (2013) indicated there is high confidence climate-induced impacts will include continued warming, changes in precipitation regimes, and more extreme weather in the Southwest, all of which will result in significant ecological impacts. Ecological responses to climate change may include changes in phenology, physiology, range, abundance and distribution, community composition, trophic interactions, and ecological structure and dynamics (Walther et al. 2002; Root et al. 2003; Parmesan 2005). Considerable evidence has been found for species' range changes and shifts in phenology (Chen et al. 2011; Parmesan & Yohe 2003).

In "Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited," Brusca et al. (2013a) compared a subset of data they collected August 5–14, 2011 from 33 0.1 hectare plots (10 x 100 meters), all in upland areas located between 3,500–9,111 feet elevation in the Santa Catalina Mountains, Pima County, Arizona (the Catalinas) with data collected in 1962–1963 by Whittaker and Niering during their classic studies of the vegetation of the mountains (Whittaker & Niering 1964, 1965, 1968a, 1968b, 1975; Niering et al. 1963, 1984; Whittaker et al. 1968). A full description of the data from which Brusca et al. (2013a) drew their subset is described in Moore et al. (2013).

Whittaker and Niering (1964) summarized species and related ecological data in a multi-page table reporting species presence in "elevation belts" of 1,000-foot increments from 3,000–9,000 feet in the Catalinas. The methodology used to construct this table is described in greater detail in Whittaker and Niering (1965, pp. 432–433). Data from the Catalinas was collected in 350 0.1 hectare quadrats (20 x 50 meters). Most plots were near the Mount Lemmon highway, but an unspecified number were in Lemmon, Pine, Sycamore, Bear, Sabino, and Pima Canyons. In addition, 80 "bajada" plots were located between 2,500–3,000 feet elevation in the Catalina foothills, including the Campbell Avenue area several miles from the highway; 50 plots were located at 9,000–

10,600 feet in the Pinaleño Mountains (some 60 miles northeast of the Catalinas); and 15 plots were at 2,400–2,800 feet in the Tucson Mountains (about 10 miles west of the Catalinas). The actual locations of all of these plots, as Brusca et al. (2013a) acknowledged, are unknown, as is the species composition of the plots.

Brusca et al. (2013a) reported elevation range changes for 27 plant species along the Catalina highway, an elevation gradient of over 5,500 feet and a distance of 20 miles, in the 50-year interval and attributed these changes to climate change. This study illustrates several problems in detecting and understanding species' range changes, tasks that require answering three basic questions: What are the actual ranges of species analyzed? How do we detect changes in them? How can we determine the cause of any changes? The following discussion is intended be a brief review of selected literature addressing these three questions, not a comprehensive review of the current knowledge of species' ranges such as that found in Gaston (2003).

United States customary units of measurement are in used below to facilitate comparison with data presented by Whittaker and Niering, Brusca et al., and other resources on the local flora.

Species ranges

Patterns of species composition and diversity are influenced by four processes: selection, drift, speciation, and dispersal (Vellend 2010). Species' ranges result from the interaction of these processes. Gaston (1991, 2003) described two measures of geographic ranges: the *extent of occurrence*, the geographic spread of a species' distribution, and the *area of occupancy*, where the species is actually found. These concepts are similar to "abiotically suitable area" and "occupied distributional area" used by Peterson et al. (2011). Both extent of occurrence and area of occupancy may include interruptions in suitable or occupied habitat resulting from factors such as topographic features and dispersal mechanisms, and both may fluctuate over time. Determining extent of occurrence can help understand the factors impacting species' range limits and to identify suitable habitats; identifying area of occupancy can help understand population dynamics, including distribution fluctuations over time (Gaston 2003). Gaston and Fuller (2009) discussed five approaches to measuring species distributions in geographic ranges: focusing on marginal occurrences, habitat distributions, range-wide occurrences, statistical modeling, and process-based modeling. They indicated that the most accurate estimates of extent of occurrence are obtained by using marginal occurrences, while the best estimates of area of occupancy are based on range-wide occurrences.

Species are neither evenly nor randomly distributed but are found in spatial structures such as patches or gradients (niches) based on many factors, including climate and topography (MacArthur 1972; Legendre & Fortin 1989; Stephenson 1990; Brown et al. 1995). In mountainous regions such as the Catalinas, habitats are highly heterogeneous, not "remarkably uniform" as Brusca et al. (2013a) claimed (see Gentry 1988; Lomolino 2001). Species assemblages in the Catalinas vary widely with elevation, topography, soils, substrate, and other factors as described by Whittaker and Niering (1964, 1965, 1968a, 1968b) and Whittaker et al. (1968). Microhabitats and microclimates (see Potter et al. 2013) significantly increase habitat complexity. Ecological niches, spatial variation in habitats, dispersal capability, and phenotypic plasticity directly impact distribution and abundance (Holt 2003; Soberon & Peterson 2005; Valladares et al. 2014). Stochastic processes such as colonization, extinction, and ecological drift also alter species' ranges (Chase & Myers 2011). Although species' ranges may be in equilibrium for considerable time, they are dynamic, expanding and contracting in response to changing abiotic and biotic drivers (Sexton et al. 2009). Determining the complete distribution of species, as well as areas of highest density, can be difficult (Sagarin and Gaines 2005; Sagarin et al. 2006). The ecological importance of peripheral or edge populations, those at some distance from the area of highest density, is unsettled (Hardie & Hutchings 2010; but see Lesica and Allendorf 1995; Hampe & Petit 2005; Slaton 2014). Numerous factors may impact the dynamics of

range limits (Gaston 2003; Sexton et al. 2009; Angert et al. 2011; Woods 2014). Small peripheral populations at the limits of a species' range may have little ecological importance unless they both persist and reproduce (Hardie & Hutchings 2010). Gaston (1991) noted that species ranges do not have true edges and that including "vagrant individuals" (isolates or outliers) can significantly alter perceived ranges. Because neither Whittaker and Niering (1964, 1965) nor Brusca et al. (2013a) assessed species' distributions and abundances, the actual elevation ranges of species in their study areas, as well as the total ranges of these species, are unknown.

Detecting range changes

Determining whether an occupied range has changed over time is complicated by the dynamic nature of species' ranges and lack of comprehensive knowledge of them. The actual distribution and abundance of species are key to understanding range dynamics (Parmesan 1996; McGill & Collins 2003; Sagarin et al. 2006), but little definitive information about them may be known. The elevation ranges determined by Brusca et al. (2013a) were based on presence-absence data in a limited portion of the species' ranges. Whether data was collected at upper and lower range limits or in the center of ranges was not determined by either Whittaker and Niering (1964, 1965) or Brusca et al. (2013a). Range change assessments based on presence at range limits may lead to erroneous conclusions because the dynamics of peripheral populations may be quite different from those at the area of highest density (Hardie & Hutchings 2010). Fluctuations in a local area may have little relationship to the dynamics of the entire range (Holt 2003) and may simply reflect normal variability within ranges. Marginal occurrence (presence data collected at range limits) is not a good measure of the actual area occupied by species unless occurrences are highly aggregated (Gaston & Fuller 2009). Strayer (1999) indicated that presence-absence data is useful when seeking to detect uniform declines throughout the ranges of common species and to detect local extinctions, particularly when a large number of sites are surveyed. Such data may not be appropriate, however, when few sites are surveyed, abundance is low, survey intensity is low, if there is high spatial variability in the population, or if declines are widespread rather than concentrated (Strayer 1999). Shoo et al. (2006) found that the minimum range changes detected in species' distributions decreased with increased sampling, that differences in sampling methods between time periods resulted in systematic bias in estimates of range shifts at upper and lower range limits, and that estimates of mean altitudes were less dependent on sampling effort than estimates of range boundaries. Archaux (2004) argued that shifts in mean elevation are indicative of population responses whereas shifts in upper and lower range limits reflect individual responses. The most accurate assessments of range changes would likely be based on significant shifts in the elevation average or mode for the species (see Kelly & Goulden 2008).

Brusca et al. (2013a) initially claimed they compared data from their plots to data from 30 Whittaker and Niering plots, but nowhere in Whittaker and Niering (1964, 1965) is there any mention of "30 plots." In their Erratum, Brusca et al. (2013b) indicated these "30 plots" were instead what Whittaker and Niering called "grouped samples" of "combined data from either 5- or 10 0.1-Ha quadrats" as shown in Whittaker and Niering's (1964) Figure 1, specifically the lettered points between 3,500 feet and 9,000 feet. The caption for that figure stated it was based on 400 samples and that "points with letters indicate mean elevation and topographic position of the grouped samples." There are 44 points with letters in Figure 1, 34 (not 30) of which are found on or between lines drawn across 3,500 and 9,000 feet markers on the y-axes. In their analysis, Whittaker and Niering (1965, p. 433) stated that within each 1,000 foot elevation belt "samples were subjected to two ordinations, or arrangements of samples in relation to gradients of environmental or community characteristics." It is unclear which type of "grouped samples" was used for Figure 1, but in any case actual elevations and species compositions of all the "grouped samples" were not reported. Thus the only Whittaker and Niering elevation data Brusca et al. (2013) could have used are those derived

from species presence in the 1,000-foot elevation belts reported in the Whittaker and Niering (1964) table which are not linked to specific plots.

Tingley and Beissinger (2009) described several problems in using historical species occurrence data to assess range changes: lack of non-occurrence and abundance data, imprecision in locating where historical data was collected, differences in historical and contemporary data collection methods, the assumption that detectability is constant over time, and the possibility of false presences or absences associated with species misidentification. Non-occurrence and abundance data are lacking for the Whittaker and Niering (1964) and Brusca et al. (2013a) data sets, the location of the Whittaker and Niering sites is unknown, the methods used by Whittaker and Niering (1964, 1965) and Brusca et al. (2013a) differed, and species identification in both studies cannot be confirmed since voucher specimens were not collected for each plot. Quantitative techniques such as occupancy modeling can correct or minimize some of these problems, but avoiding bias requires "at a minimum" repeated visits within sampling periods and data from a sufficient number of sites to achieve adequate statistical power (Tingley & Beissinger 2009).

Identification of differences in the highest and lowest elevation presence of 27 "common" plant species between those reported by Whittaker and Niering in 1962–1963 and those recorded by Brusca et al. in 2011 is not evidence of range changes in the Catalinas, or even along the Catalina Highway, because of the small number and location of Brusca et al. (2013a) plots. Brusca et al. (2013a) used "common" to refer only to presence of a species in five or more plots; the term is not an indication of the abundance or distribution of these species either along the highway or the mountain range as a whole. Having studied vegetation in a major drainage in the Catalinas, during more than 1,460 field trips in over 30 years, I am very surprised that only 27 species would be found in five or more plots if these plots were at all representative of the constantly changing vegetation along the highway, particularly when this list does not include a number of abundant species found in the area. Both presence and absence of a species could be a chance occurrence, particularly when sample size is small. Small sample size also prevents determination whether individuals of selected species represent isolates, peripheral populations, or the core population. Soberon and Peterson (2005) indicated that absence data is more likely to result from lack of data or insufficient sampling than actual absence unless the data has both high resolution and density. Consequently the number of plots surveyed is crucial. Absence data from the 33 Brusca et al. (2013a) plots (about 5 per 1,000 feet elevation) is much less likely to reflect true absence than such data from the 350 plots (55–60 per 1,000 feet elevation belt) of Whittaker and Niering (1964).

It is especially problematic that Brusca et al. (2013a), unlike Whittaker and Niering (1964, 1965), did not sample riparian or xeroriparian areas characterized by permanent, ephemeral, or intermittent streams. Whittaker and Niering (1964) included plots in topographic categories described as "deeper ravines or canyons with flowing streams" and "shallower draws and lower slopes of canyons." In their table, over 40% of the species listed were found in each of these topographic areas and more than 60% were found in one or both. Plants listed in the table also include several aquatic species. Yet Brusca et al. (2013a, p. 3309) justified their use of only upland plots by the claim that Whittaker and Niering data "are sparse for riparian/'wet canyon' sites." In restricting their plots to upland areas, Brusca et al. (2013a) introduced significant sampling bias (see Chytry et al. 2014). Diversity in riparian and xeroriparian habitats is often greater than that of the surrounding uplands, and many species are found at their lowest elevation limits in them (Naiman & Dechamps 1997; Levick et al. 2008). Two canyons in the front range (southern portion) of the Catalinas, one xeroriparian and one riparian, illustrate the diversity of such systems: approximately 50% of the 1,200 taxa included in the Southwest Environmental Information Network (SEINet 2014) species list for the Catalinas has been found in the xeroriparian Finger Rock Canyon drainage, a gradient of 4,158 feet that includes less than 1% of the area of the Catalinas (unpublished personal data); in lower Sabino Canyon, a riparian area between 2,700–3,600 feet elevation, about 40% of the

taxa known from the Catalinas has been identified (Joan Tedford, unpublished data). The flora checklists for both areas are based on more than 30 years of collection and observation.

Available data on species' ranges in the Catalinas is limited because the range has been under collected, in part because of the rugged topography. Arizona herbaria specimens for the Catalinas included in SEINet do not always include elevation data, and locations may be imprecise. Available data was collected by many different individuals, using different survey methods and various means of assessing elevations, over widely different time periods for different purposes. A comparison of the elevation ranges for the 27 species analyzed by Brusca et al. (2013a) with those reported by Whittaker and Niering (1964), Bowers and McLaughlin (1987) for the adjacent Rincon Mountains; and Kearney and Peebles (1960) for the state of Arizona show considerable variation. In each case, these elevation ranges are little more than "best guesses" of the actual ranges of these species because comprehensive surveys of total ranges in the respective areas, including assessment of abundances and distributions, were not made. Whittaker and Niering (1964), for example, reported *Juniperus deppeana* Steud. (alligator juniper) in the 3,000–4,000 feet elevation belt up to the 7,000–8,000 feet belt. Brusca et al. (2013a) reported an elevation range of 5,028 feet to 7,162 feet for the species, Bowers and McLaughlin (1987) reported a range of 4,200 feet to 8,400 feet, and Kearney and Peebles (1960) reported a range of 4,500 feet to 8,000 feet. The methods for determining altitude were not reported by any of these researchers. Recently a large alligator juniper, 47 inches in diameter at the base, was vouchered in Sabino Canyon (ARIZ 416153, University of Arizona Herbarium). By plotting GPS latitude-longitude coordinates on a 7.5 minute topographic map using ArcMap, the elevation was determined to be 2,750 feet. It is conceivable this very tree was the basis for presence of the species in Whittaker and Niering's 3,000–4,000 feet belt given that some of their plots were located in Sabino Canyon.

Without accurate knowledge of the actual ranges of the species analyzed and an understanding of core and peripheral populations, real change cannot be detected. There is certainly no evidence of change in the Brusca et al. (2013a) plots because data was collected at only one point in time. The Whittaker and Niering (1964) data cannot be considered a proxy for presence-absence of species in the Brusca et al. (2013a) plots 50 years ago because the locations of the Whittaker and Niering plots are unknown and because at least some of the Whittaker and Niering plots were located in large drainages at some distance from the highway. Chytry et al. (2014) demonstrated the difficulty in using data from historical plots even when the exact location of these plots is known. They further showed that comparing data from historic and new plots in different locations is "a risky business," and stated that any results must be interpreted with "the utmost caution." Errors may include detecting change when change did not actually occur, not detecting change that did occur, and detecting change in a different direction or magnitude of the real change (Chytry et al. 2014).

Determining causes of range changes

Detection and attribution of climate change impacts is challenging and usually requires significant observation over several decades (Parmesan et al. 2011; Stone et al. 2013; O'Connor et al. 2014). Species may "follow" their ecological niche when that niche moves due to changing climate (Martínez-Meyer & Peterson 2006; Van der Putten 2012), but range changes may occur in the absence of directional environmental change (Holt 2003). Few studies have documented species' range shifts directly; rather most have inferred shifts from observations at local range extremes or from changes in species composition in a limited community (Parmesan 2007). Epstein et al. (2004) reported that in the arctic, where the most rapid warming is occurring, it may be "difficult, if not impossible" to distinguish whether vegetative responses result from climate change or climate variability without at least 20 years of field studies. Brusca et al. (2013a) concluded from their analysis of a very small number of species in a very small area that "rapid vegetation change" is occurring in the Southwest and described this change as "dramatic." This is hyperbole at best.

Relatively brief observations at two different time periods in relatively limited area is insufficient to demonstrate that real change has occurred without knowledge of climatic conditions and population demographics (time of establishment, abundance, size, age structure, reproduction, etc.) of species at their elevation limits at both points in time. Has change occurred elsewhere in the ranges of species studied? Is the change temporary or permanent? Did the change occur during normal climatic conditions or during particularly optimal or adverse conditions? Was the change due to loss or addition of a robust population or a few individuals? Was a lost population the product of opportunistic colonization during climatically favorable conditions or was it a long-established population adapted to local climate variability? These are only some of the questions that must be addressed before assessing the significance of perceived change or attributing it to any cause.

Even if Brusca et al. (2013a) had resurveyed 33 of the actual plots surveyed by Whittaker and Niering (1964, 1965) and change was documented, the causes of any perceived change cannot be determined without knowing natural and human impacts in the study area over the 50-year period (see Slaton 2014; Angelo 2014a, 2014b). Potential causes for variations in species' ranges in the Catalinas include climate variability; surface disturbances such as water and wind erosion, debris flows, and fire; interspecific interactions such as competition, mutualism, and facilitation; and human activities, such as recreation, habitat conversion, introduction of invasive species, and road maintenance, construction, or reconstruction.

Precipitation and temperature in the Southwest over the last 400 years have been highly variable (Sheppard et al. 2002; Griffin et al. 2013). Continued observation over time is essential to determine the nature and impact of this variability. Brusca et al. (2013a) used mean annual temperature and mean annual precipitation to show climate trends. This is problematic because biotic responses to both climate variability and climate change result from highly complex interactions among climatic factors (Dobrowski et al. 2013). Mean temperature and precipitation values mask seasonal differences and resulting impacts (Stephenson 1990). Obtaining a good measure of climatic variability in the Catalinas is difficult because long-term local data is not available and because precipitation and temperature are strongly influenced by the topography and elevation gradient of the mountains (Shreve 1915; Whittaker & Niering 1965). Brusca et al. (2013a) used data from the National Weather Service station at the Tucson International Airport. The station is located on a valley floor several miles from the Catalinas, at an elevation of 2,546 feet; consequently, it is likely a poor proxy for climate in the mountains, particularly at middle and higher elevations. Weather data based on the Parameter-elevation Relationships on Independent Slopes Model (PRISM) described by Daly et al. (2008) is physiographically sensitive and is available for 1895 to present; PRISM would be a better source for approximating temperature and precipitation in the Catalinas. Seven years' data from three rain gages at 3,100 feet, 4,920 feet, and 7,250 feet in my study area in the Finger Rock Canyon drainage of the Catalinas indicate that PRISM data overestimate precipitation at lower elevations, underestimate precipitation at higher elevations, but provide a fairly accurate estimation of precipitation at middle elevations. PRISM data closely reflect the pattern (relative amount and spacing) of precipitation in the drainage and provide a far more accurate approximation of precipitation over the elevation gradient than Tucson International Airport data.

Some of the plants defining the range extremes 50 years ago may have germinated and lived for a time under optimal climatic conditions and then died when conditions returned to normal or worsened significantly. Droughts are cyclical in the American Southwest, and major droughts occurred in the early 1900s and 1950s (Sheppard et al. 2002). Since the late 1990s the area has experienced persistent drought accompanied by warmer than normal temperatures (Woodhouse et al. 2010). Drought alone could explain any changes in elevation that might have occurred in the last 50 years. When drought conditions ease, particularly if optimal conditions follow, plant ranges could expand.

Although climate variability is the most likely cause of short-term changes in species ranges, natural and human caused surface disturbances cannot be discounted. These disturbances, with the exception of non-native species invasions and major fires, are usually limited to fairly small areas, but the areas affected could have been the very plots studied by Whittaker and Niering or Brusca et al. Significant runoff during major storm events such as those that occurred in the winter of 1992–1993 and the summer of 2006 in the Catalinas may remove vegetation on steep slopes and shallow drainages and can scour riparian areas (Naiman & Dechamps 1997; Levick et al. 2008). Debris flows, commonly known as rock slides, such as those that occurred in the Catalinas in 2006 can cause extensive change on steep slopes and canyon bottoms (Youberg et al. 2008). Recreational uses such as camping or hiking can eliminate vegetation through trampling, soil compaction, or harvesting. Such uses may be of particular importance since most of the Whittaker and Niering (1964) plots and all of the Brusca et al. (2013a) plots were near the heavily traveled highway. Additionally, significant reconstruction of the highway has occurred in the last 30 years, and off-highway vehicular travel has increased.

Given high climate variability in the Southwest over the last 5,000 years (Ely et al. 1993), attributing short-term changes in average temperature and precipitation, or short-term vegetative changes of a few species, to climate change is highly problematic given both the resolution and time span of available data (Gaston 2003). As Overpeck et al. (2005) noted, "Climate variability and change during the past century have been modest relative to alterations in the climate system in the past." Vegetative communities may be relatively stable over long periods, but the composition of these communities continually changes during normal climate variability (Sexton et al. 2009). It seems highly likely that if climate change is impacting vegetative communities, there would be multiple responses over time, including changes in (a) onset, duration, and end of flowering, (b) flowering ranges, (c) species composition and structure, (d) abundance and distribution, (e) species' elevational and geographic ranges, (f) trophic mismatches, and (g) reproductive success. Moreover such changes would be expected in a significant portion of species' ranges. Identifying multiple climate-related responses over a broad area during an extended period of time would increase confidence in a conclusion that climate change is an actual driver (Root et al. 2003; Angelo 2014a, 2014b). With any degree of certainty, we can only say that short-term change in one response over a few decades is consistent with what we might expect with a changing climate.

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Spellenberg, R. 2014. *Quercus barrancana* (sect. *Quercus*, white oaks), a new species from northwestern Mexico. Phytoneuron 2014-105: 1–12. Published 12 November 2014. ISSN 2153 733X

QUERCUS BARRANCANA (SECT. *QUERCUS*, WHITE OAKS), A NEW SPECIES FROM NORTHWESTERN MEXICO

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ABSTRACT

Quercus barrancana Spellenb., **sp. nov.**, a white oak (sect. *Quercus*), is described from southwestern Chihuahua and southeastern Sonora in northwestern Mexico. It is a small-leaved evergreen oak primarily of the barranca (canyon) country on the west slope of the Sierra Madre Occidental. The new species differs from the more northern *Q. toumeyi* Sarg. by having most leaves on the tree usually toothed on their margins and the adaxial surfaces bearing spirally contorted multirayed hairs. It is a small tree or shrub, finding some use as firewood. The acorns are eaten by indigenous people.

From the start of our explorations of the flora of the northern Sierra Madre Occidental in the early 1980s, we have been aware of a well-defined southern population of a white oak (sect. *Quercus*) usually identified as *Quercus toumeyi* Sarg., occasionally as *Q. arizonica* Sarg., or as annotated by J. Tucker on a few large-leaved specimens at DAV, as an intergrade between the two species. In a review of oaks of the region (Spellenberg 2001a) this oak was included within *Q. toumeyi*, with distinctions briefly explained for this southern population. Since that time it was necessary to return specimens borrowed from other herbaria; these were annotated as "*Q. toumeyi* southern phase" or "*Q. barrancana*" as a name *med.* For a short period I considered this southern population to be best considered as a variety. Finally, however, this small oak is recognized as a species closely allied to *Q. toumeyi*, a view consistent with a species concept for oaks as proposed by Nixon (1993). The distinctions of the new species formally recognized here were commented upon by Felger et al. (2001), where he discussed differences between northern and southern races of *Q. toumeyi*.

QUERCUS BARRANCANA R. Spellenberg, **sp. nov**. (Fig. 2).

TYPE: MEXICO. Chihuahua. Mpio de Guachochi: 50 km S of of Creel, 13 km N of crossing of Río Urique, 6.5 km N of Humira, E of present highway Mex. 23, along old road, 27º 26' 58.6" N; 107º 29' 21.9" W, elev. 2115 m, 28 Aug 2004, *R. Spellenberg and W. Anderson 13487* (holotype: NY; isotypes: ARIZ, CIIDIR, IBUG, IEB, MEXU, NMC, NY, TEX, UC, US, USON). The type collection *13487* encompasses a small population sample made at the same time and same place, but from different trees in the population, each tree designated by a letter (a-f). To help locate specimens in the future and associate them with others of the series, the distribution of this collection is as follows: MEXU, NY (tree a); NMC, TEX (tree b); US (tree c); MO, USON (tree d); CIIDIR, IBUG (tree e); ARIZ, IEB UC (tree f).

Quercus barrancana is similar to *Q. toumeyi* in habit and features of flower and fruit. Both species inhabit dry rocky sites. *Quercus barrancana* differs by features of leaf margin dentation and pubescence of the abaxial leaf surface, and to a lesser extent in leaf shape. The small, toothed leaves, small acorns, and the contorted multirayed hairs also distinguish *Q. barrancana* from other oaks in the region.

Shrubs or small trees 1–5 m tall with one to several trunks 3–15 cm diam., often contorted, sometimes sprouting from stumps, the crown round or broadly oval, 1–6 m broad, the branches ascending to spreading (Fig. 4). **Twigs** shaggy-pilose with loosely appressed and a few spreading

stellate hairs with crinkled branches in first year; more sparsely pubescent in second year; glabrous or glabrate in third, the surface reddish brown and becoming shallowly fissured, flaking on larger branchlets. Lenticels raised, whitish, ca. 1 mm diam. on 3rd-year twigs. Buds broadly oval to globose, 1 mm long, bronze-orange, lustrous, lightly to moderately pubescent with crinkled hairs on margins of bud scales. **Foliage** evergreen (may be drought deciduous) dense, dark green. **Leaves** oval, narrowly ovate, oblong, oblong-elliptic, or slightly obovate (Fig. 5, 6), 12–36 mm long, 6–15 mm wide (up to 40 mm long, 18 mm wide on fast-growing shoots), base rounded to shallowly cordate, tip obtuse to rounded, with a low callus-tipped point, margin usually with at 1–4 low teeth in two-thirds of blade, each tooth with a callus-tipped point. Marginal teeth 0.5–1 mm high (2–3 mm on leaves from fast growing young shoots), asymmetric and forward pointing (steeply ascending on side toward leaf tip, gradually ascending on side toward leaf base). Young leaves densely pale pubescent with spreading, multi-multirayed hairs on both surfaces, those near the margin and over the midvein often reddish, the hairs decreasing in density as leaf ages. Adaxial surface of mature blade with scattered multirayed crinkled hairs or glabrate, lustrous, with a prominent slightly depressed central vein and weaker lateral veins, the veinlets pale, forming a reticulum even with surface of blade. Abaxial surface of blade dull, the midvein prominently raised, the lateral veins less so, the veinlets inconspicuous; surface sparsely to moderately pubescent with often spirally contorted multirayed hairs and appressed, often sparse, pale whitish or yellowish glandular vermiform hairs (Fig. 7). Veins 5–9 on each side of blade, ending in reticulum of veinlets near teeth or margin, more or less anastomosing through looping smaller veinlets. **Staminate catkins** greenish yellow (appearing late March through early June), slender, spreading or pendulous, 18–23 mm long, 3 mm diam., the axis sparsely to densely pubescent with spreading crinkled hairs, bearing 10–15 flowers; involucre 4–5 lobed, 0.9–1.3 mm long, the lobes lance-ovate, ovate, oblong, to nearly round, free for 1/2–2/3 length, crinkly pilose on back, the margin irregularly toothed or ± entire, or entire but lacerate at tip, ciliate with crinkly hairs 02.–04 mm long that are sometimes reddish; stamens from 3 to usually 5 per flower, filaments 0.5–1.5 mm long, anther 1–1.5 mm long, greenish yellow. **Acorns** maturing from late June to mid-September, fusiform, olive brown, 12–19 mm long, 8–10 mm wide, approximately 1/4–1/3 covered by cap (Fig. 8); involucre 4–7 mm high, 6–11 mm wide, yellowish brown, densely short-tomentose, the center of the scales glabrous or glabrate, usually borne singly on peduncles 1–4 long, occasionally in clusters of 2–6 on peduncles up to about 2 cm long.

Igneous, rocky, slopes and banks, at 1300-2115 m elev., with *Agave, Ageratina, Arbutus, Bidens, Muhlenbergia, Opuntia, Stevia, Pinus chihuahuana, Pinus engelmannii, Juniperus* etc., in dry oak woodland or pine-oak woodland, often forming thickets (Fig. 1, 4). Commonly associated with, or in vicinity of, *Q. chihuahuensis* Trel., *Q. grisea* Liebm., *Q. arizonica* Sarg., *Q. jonesii* Trel., *Q. mcvaughii* Spellenb., *Q. oblongifolia* Torr., *Q. tarahumara* Spellenb., Bacon, & Breedlove, and *Q. viminea* Trel.

The epithet "*barrancana*" refers to the habitat of the species. Much of its range is in the large, steep walled, rocky canyons (*barrancas*) in eastern Sonora and western Chihuahua, on the west slope of the Sierra Madre Occidental.

Geographic range

Quercus barrancana is found in northwestern Mexico from Mpio. de Tomósachi (Chihuahua) and Mpio. de Yécora (Sonora) southward to Mpio. de Alamos (Sonora) and Mpio. de Guachochi (Chihuahua) (Fig. 3).

The range of *Quercus toumeyi* (Fig. 3) lies to the north in the Sierra Madre of Mexico and in the Sky Island region (USDA Forest Service 1995) in the southwestern USA, extending from Pima, Cochise (Arizona), and Hidalgo (New Mexico) counties at the northern end of its range to municipios de Yécora (Sonora) and Madera (Chihuahua) in the south. The presence of *Q. toumeyi* in extreme western Texas, as related by Nixon and Muller (1997), is apparently based upon a small set of

collections from the northern Quitman Mountains, at the south end of Smuggler's Gap, in Hudspeth Co., made on 15 Jun 1976 (*Butterwick & Lamb 2720, 2721, 2722*, LL). These have small, broadly lanceolate leaves characteristic of *Q. toumeyi* but have soft stellate hairs on the abaxial surface in addition to pale, glandular vermiform hairs. They may represent forms of *Q. turbinella* Greene with small toothless leaves, resulting from introgression with *Q. grisea* Liebm. I cannot, however, exclude them from introgressed *Q. toumeyi*. Similar plants also occur to the north, in the Franklin Mts. of El Paso Co., made on 27 July, 1989 (*Spellenberg 9982*, BRIT, MEXU, MO, NMC, NY, SRSC, TEX, US, UTEP). While making that collection I found no plants that were "good" *Q. toumeyi*.

Putative relationships and taxonomic rank

Hybridization and intergradation among oak species is common (Nixon 1993), as it is in the Sierra Madre Occidental (Spellenberg 2001b), usually surmised to be occurring by the presence of trees intermediate between two more widespread morphologically different species. The same holds for *Quercus barrancana* in eastern Sonora and western Chihuahua in its area of contact with *Q. toumeyi*. Intergrades are listed in specimens cited. These intergrades have comparatively broad leaves with few or no teeth and a reduced density of contorted branched hairs on the lower surface. Some specimens of *Q. chuchuichupensis* Muller, cited by Muller, are among these intergrades (see discussion of these specimens below, in the specimens cited section). LeSeuer's specimens form the type collection and represent *Q. toumeyi*.

Vernacular name and human uses of *Quercus barrancana*.

Occasional specimens give vernacular name and/or human uses, the collector often learning this information from a local associate. Names I have seen on specimens of *Quercus barrancana* are these: *ncino chakira* (Sonora, language not stated; *Sanchez-Escalente s.n.*); *makóchare* (Chihuahua, Tarahumara: *Bye 5604*; *pechirt*, Tarahumara, (*Bye 6123*), *péchort* (*Bye 5613*), *péchurt* (*Bye 6199*), *epécharı* (*Bye 5816*); Spanish, *cacachila* [Chihuahua, *D. Yetman, M. Kalb, N. Tadea s.n.* (ARIZ) - also the common name for *Karwinskia humboldtiana* (Schult.) Zucc., which the oak somewhat resembles (pers. comm. D. Yetman.)]. *Quercus barrancana* is used for firewood, the bark to fire "ollas" (*Bye 5604*), acorns are used in *esquiate* (*Bye 6123*), and acorns are eaten raw (a little bitter) or ground and washed before consumption (*Bye 5613*).

ACKNOWLEDGEMENTS

Over the decades that have passed since we understood that this oak represented a new taxon, numerous people have provided help with this little, slow-birthing project. I am indebted to patient curators who sent loans long-held at NMC. Numerous students helped with field work in Mexico, all of whom were good sports and great fun to be with. Among them, particularly, were Rob Soreng, an indefatigable and enthusiastic field companion, and Jeff Bacon, a student of the oaks who could roll with the punches of field work with good humor. Colleagues Toutcha Lebgue, from the Universidad Autonoma de Chihuahua, who studies native plants of Chihuahua, James Zimmerman, a gall wasp specialist, and William Boecklen, who studied co-evolution of oaks and their parasites, the latter two individuals from New Mexico State University, were welcome participants on many trips. A good friend, Wynn Anderson, went with me on several trips to the Sierra Madre Occidental in Chihuahua and on one of them we serendipitously collected the type specimen when we were faced with fruiting trees of the new species at a rest stop. My wife, Naida Zucker, provided invaluable help with preparing the distribution map. Jennifer Thorsch facilitated a pleasant visit to USCB to view the type of *Quercus chuchuichupensis*. Guy Nesom helped with questions regarding typifying the new taxon, provided constructive comments on the manuscript, and much earlier searched for specimens of *Q. toumeyi* from western Texas that might be housed at TEX.

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Representative specimens of *Quercus barrancana*. Fruiting specimens are indicated by *, flowering specimens by **

CHIHUAHUA. Mpio. de Batopilas: S of Quirare, N of Barranca de Batopilas, ca. 1890 m elev., 27 Oct 1973, *Bye 5604* (DAV); near abandoned Milpa S of Quirare, N rim of Barranca de Batopilas, ca. 6300 ft elev., 27 Oct 1973, *Bye 5613* (ECON); old milpa, S of Quirare (2 mi along road), elev. 5900 ft., 19 Jul 1974, *Bye, Jr. s.n.* (ECON); between Basigochic and Quirare, 2165-1980 m elev., 4-6 Jan 1974, *Bye 6123* (DAV, ECON); 4 km SW of junction of Creel – Guachochi road on road down to La Bufa, 13 Sep 1986, *Spellenberg & Zimmerman 8610* (CAS, INIF, MEXU, NMC, NY)*; Loreto, 18 May 1998, *Yetman & Kalb s.n* (ARIZ); Loreto, 14 May 1998, *Yetman, Kalb, Tadea s.n.* (ARIZ). Mpio. de Chinipas: Mpio. de Guazapares – Chinipas, near ranchito Nopalero, E slope of Barranca de Chihipas, ca. 4000 ft. elev, 9 Nov 1973, *Bye, Jr. 5816* (ECON); Rancho Byerly, Sierra Charuco, 5000-5800 ft, 17-25 Apr 1948, *Gentry 8029* (ARIZ), *8148* (ARIZ); Rancho Byerly, Sierra Charuco, summer of 1946, *Maj. Langille 3* (ARIZ), *11* (ARIZ, NMC), *12* (ARIZ); Rancho Quemado (=Rancho Byerly), close to Sonoran line, 27°34'30"N, 108°41'40"W, elev. 5300 ft, 20 May 1986, *Martin s.n.* (ARIZ). Mpio. de Guachochic: KM48+5 on new Creel – Guachochic road near pass between Basihuare and Humirá, 6400 ft. elev., 12 Jan 1974, *Bye, Jr. 6211* (DAV, ECON); above pass between Basihuare and Humirá, along trail to large cave near Cuevas de las Caballos, 6500 ft. elev., 12 Jan 1974, *Bye, Jr., 6212* (DAV, ECON); 17 air mi/ 28 road mi SSE of Creel, 2 mi S of Basehuare, 107°30"W, 27°26'N, elev. 6400', 15 Apr 1984, *Spellenberg & Soreng 7719* (DAV, NMC); 40 km S of Creel, 19 km S of Cusarare, 13 km N of Humira, on road to Guachochi, 4 Oct 1986, *Spellenberg & Zimmerman* 8600 (CAS, INIF, MEXU, NMC, NY); on the Creel – Guachochic road 62 km S of Creel, 5 km S of Humira, at the crossing of the Río Urique. elev. 1610 m., 16 Jun 1993, *Spellenberg, Broullet, & Ulaszek 11834* (MEXU, NMC, MT); 51 km S of Creel, 12 km N of crossing of Río Urique, on Mex. Hwy. 23, 27º 26", 52.6" N, 107º 29' 18.8"W (ca. 1 km S of type locality), 2025 m

elev., 28 Mar 2009, *Spellenberg & Anderson 14071* (MEXU, MO, NMC)**. Mpio. de Guerrero: San Isidro, 1768 m, 29 Jun 1970, *Pennington 23* (DAV) [municipality estimated, not given on specimen and is uncertain]. Mpio de Madera: km 279, hwy 16 to Madera, W slope of Sierra Chinaca, km 279, 108°18'53.0"W, 29°12'08.4"N, 5 Aug 1998, *Bacon, Vázquez-Villagran, & Phillips 5335* (NMC [indicated on label also to be distributed to BH, CIIDIR, F, IBUG, MEXU, MO]); est. 28 air km WSW of Madera, 35 rd. km E of the Río Tutuaca on the road to Sirupa on the road from an abandoned mining complex, Dolores. Est. 29°10'N, 108°29'W, elev. 1860 m., 19 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9799* (ARIZ, CIIDIR, MEXU, NMC, NY, TEX, RSA); est. 29 air km WSW of Madera, 22 km E of Río Tutuaca, on road to Dolores, elev. 1830 m., 19 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9806* (MEXU, NMC). Mpio. de Maguarichic: Maguarichic, 5 April 1940, *Knobloch 7094* (TEX); 34 km from the Basaseachic – San Juanito Rd, 3.5 km NE of Maguarichi, elev. 1750 m, 27 Apr 1985, *Spellenberg, Soreng, & Corral 8091* (BH, CAS, CIIDIR, MEXU, NMC)**. Mpio de Matachic: near km 9.7 of Matachic-Cocomariachic road, 1900 m elev., 29 Aug 1978, *Bye 9015* (DAV). Mpio. de Moris: near km 43 on road from Ocampo to Moris, 28.9°20'N, 108°27'20"W, 5 Jul 1985, *Martin & Duek s.n.* (ARIZ)*; 1 mi E of El Pilar, 17 mi W of Moris, elev. 4900 ft., 14 Sep 1987, *Spellenberg & Jewell 9391* (CAS, MEXU, NMC, NY)*; 4 road mi E of Moris, 16 mi W of Ocampo, 14 Sep 1987, *Spellenberg & Jewell 9400* (CIIDIR, MEXU, NMC). Mpio. de Ocampo: Parque Nacional Cascada de Basaseachi, 28° 10", 23" N, 108° 14' 01"W, 2000 m elev., 7 Oct. 2009, *Joe & Cortes 1140* (NMC); Candameña Barranca transect on road from Cruz Verde to Candameña River, 18 Mar 1988, *Donohoe 58* et al. (ARIZ); Basaseachic Falls, S rim overlook, 2000 m elev., 28° 09'10"N, 108°12'40"W, 6 Jul 1985, *Martin s.n.* (ARIZ); Ocampo mine site, 28°10'40"N, 108°22'40"W, 1800 m elev., 25 Jun 1986, *Martin s.n.* (ARIZ)**; Cascada de Basaseachic, headwaters of the Rio Mayo, 28° 10' 20"N, 108°13'W, elev. 1900 m, 25 Feb 1987, *Martin et al., s.n.* (ARIZ); along drainage of Río Basaseachic at Cascada de Basaseachic, ca. 1 mi S of village of Basaseachic, elev. ca 2000 m., 14 Oct 1984, *R. & M. Spellenberg 7903-A* (DAV, MEXU, NMC, NY); Parque Nacional de Cascada Basaseachic, elev. ca. 1800 m, 4 Oct 1986, *Spellenberg, Soreng, Corral, & Lebgue 8830* (NMC); Parque Nacional de Cascada Basaseachic, elev. ca. 1800 m, 25 Apr 1987, *Spellenberg, Corral, & Columbus 9071* (NMC)**; Parque Nacional Cascada de Basasechic, near campground above falls, 1 Aug 1988, *Spellenberg 9643-C* (NMC); Pinos Altos, ca. 15 air km NNE of Ocampo, elev. 2100 m., 22 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9827* (MEXU, NMC); ca. 150 m below Cruz Verde (rim of the barranca) on the old road from near Huajumar to Candameña, elev. 1675 m., 27 Jun 1991, *Spellenberg & Martin 10817* (MEXU, NMC)*; Cruz Verde (rim of the barranca) on the old road from near Huajumar to Candameña, 108°17' W, 28°06' N, elev. 1950 m, 25 Jun 1991, *Spellenberg & Martin 10827* (ARIZ, MEXU, NMC); ca. 8 km by winding road E of Ocampo, 108°19'W, 28°11"N, elev. 2060 m, 25 Sep 1991, *Spellenberg, Boecklen, & Gregory 10907* (CIIDIR, NMC); Parque Nacional de la Cascada de Basaseachic, elev. 1980 m., *Spellenberg, Boecklen, & Gregory 10925* (NMC). Mpio. de. Temósachic: Nabogame, 28°30'N, 108°30'W, elev. 1800 m, 28 Jul 1987, *Laferriére 541* (NMC)*; Río Cocheño crossing, Hwy. 16, 28° 21'N, 108°19'W, 1550 m elev., 15 Aug 1987, *Martin, Krzyzanowski, & Martin s.n.* (ARIZ) same locality and date, *Martin et al., s.n.* (ARIZ); ca. 45 km due W of Cd. Guerrero, Sierra Chuchupate, 2.5 mi NE of Tosanochic, 107°59'W, 28°30'N, 13 Apr 1984, *Spellenberg & Soreng 7685* (DAV, NMC); 27 km W of jct. of road to Ocampo with Basaseachic – Yepachic road, on road to Yepachic. elev. 1800 m., 22 Jun 1989, *Spellenberg, Boecklen, Zimmerman 9831* (CAS, CIIDIR, MEXU, NMC, TEX), Chihuahua, Mpio. de Temósachic, 14 km E of Sonora border, 28°27'N, 106°26'W, elev. 1645 m., 23 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9853.1* (ASU, BRIT, CIIDIR, MEXU, NMC, NY, TEX, US). Mpio. de Urique: S side of bridge over Río Urique, between Humirá and Napuchi, elev. ca. 5100 ft, 12 Jan 1974, *Bye, Jr. 6169* (ECON), *6179* (ECON); Mpio de Urique – Guachochi, N rim of Barranca del Cobre, between Humirá and Divisadero, ca. 5900 ft. elev., 12 Jan 1974, *Bye, Jr. 6197* (ECON), *6199* (ECON); km 627.3 road to Urique, elev. 1880 m, 107°56'31.1"W, 28°56'31.1"W, 7 Aug 1998, *Bacon, Vázquez-Villagran, & Phillips 5382* (NMC [indicated on label also to be distributed to BH, CIIDIR, MEXU]); km 775 on

road from Bahuichivo to San Rafael, elev. 2330 m, 107°30'08.3"W, 27°31'39.6"N, 7 Aug 1998, *Bacon, Vázquez-Villagran, & Phillips 5382* (NMC [indicated on label also to be distributed to BH, CIIDIR]). **SONORA**. Mpio. de Alamos: 1 km E of El Chiribo, 27° 18' N, 108° 42' W, 20 Aug 1991, *Martin & Yetman s.n.* (ARIZ); 39.2 km ENE of Alamos (by road), 3.1 km below (SW) Rancho Santa Barbara, 27° 06' 47" N, 108° 44' 13" W, 1310 m elev., 15 Jan 2008, *Sánchez-Escalante s.n.* (NMC): same site, 7 Oct 2006, *Martin s.n.* (ARIZ); same site, 7 Oct. 2006, *Reina G. et al. 2006-1275* (NMC). Mpio. de Yécora: 33 km W of Maycoba on road to Yécora, 28° 21' N, 108° 50' W, elev. 1460 m., 23 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9876* (CIIDIR, MEXU, NMC, TEX); on road between Tecoripa and Yécora, 17.6 km E of Santa Rosa toward Yécora, elev. 1525 m., 24 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9876* (ARIZ, MEXU, NMC); 5 km W of Yécora, 1645 m, 24 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9890* (BRIT, MEXU, NMC, UC)*; along Arroyo El Kipor (Quipor), Cordon Las Taunas, from El Kipor E to Tierra Panda (Las Taunas), elev. 1740 m, 10 Sep 1995, *Van Devender 95-989 with Reina G. & Fourns* (ARIZ).

Specimens intermediate between *Quercus barrancana* and *Q. toumeyi*. Leaves mostly entire, often small, but with a few contorted hairs.

CHIHUAHUA. Mpio. de Madera: km 279, hwy 16 to Madera, W slope of Sierra Chinaca, km 279, elev. 1920 m, 108°18'53.0"W, 29°12'08.4"N, 5 Aug 1998, *Bacon, Vázquez-Villagran, & Phillips 5336* (NMC [indicated on label also to be distributed to BH, CIIDIR, IBUG, MEXU, MO]); km 279, hwy 16 to Madera, W slope of Sierra Chinaca, km 279, elev. 1920 m, 108°18'53.0"W, 29°12'08.4"N, 5 Aug 1998, *Bacon, Vázquez-Villagran, & Phillips 5336* (NMC [indicated on label also to be distributed to BH, CIIDIR, MEXU]); km 280.5, hwy 16 to Madera, W slope of Sierra Chinaca, km 280.5, elev. 1940 m, 108°19'02.3"W, 29°12'27.5"N, 5 Aug 1998, *Bacon, Vázquez-Villagran, & Phillips 5339* (NMC [indicated on label also to be distributed to BH]); 25 mi s.w. of Chuhuichupa, on trail to el Rio Bonito; common with the species, shrub form of #3600, 2 Oct 1939, *Muller 3601A* (LL); same locality, tree form of #3601, common with the species, *Muller 3601B* (LL); 29 mi SW of Chuhuichupa on trail to el Rio Bonito, shrub to 6 ft. or small tree to 6 in. x 15 ft. with scaly soft grey bark, abundant locally on dry open ridge tops on w. slope of the Sierra Madre, 2 Oct 1939, *Muller 3601* [Muller's IDs on 3601, 3601A, and 3601B are all *C. chuchuichupensis* C. H. Mull. Note that even though the Muller specimens cited above may be considered intergrades, the holotype (USCB!) and isotype (TEX!) of *Q. chuchuipensis* have entire (rarely 1 tooth on a side), narrowly acute and apiculate, proportionately narrow (30x10 mm to 21x7 mm) leaves with slightly undulate margins, the abaxial surface with only sparse, golden, vermiform hairs, and are considered to be "good" *Q. toumeyi*; Sierras W of Chuhuichupa, 28 Aug 1936, *LeSueur Mex-525*]. Mpio de Temósachic: 11 km W of Yepachic, ca. 14 km E of Sonora border, 28°27'N, 106°26'W, 23 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9853.2* (CIIDIR, MEXU, NMC, NY, TEX) [this population had intergrades to *Q. oblongifolia* (see below), and also has "good" Q. *barrancana, Spellenberg, Boecklen, & Zimmerman 9853.1* (ASU, BRIT, CIIDIR, MEXU, NMC, NY, TEX) and *Q. toumeyi, Spellenberg, Boecklen, & Zimmerman 9853.3*; (CIIDIR, MEXU, NMC, NY, TEX). **SONORA**. Mpio. de Yécora: Maicoba, 1675 m, 29 Jun 1958, *Pennington 106* (DAV); Maicoba, 1675 m, 9 Jul 1968, *Pennington 162* (DAV); 7.7 km W of Maycoba on road to Yécora, elev. 1465 m, 23 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9869* (BRIT, MEXU, NMC) [collection mixed, with "good" *Q. barrancana* and a few plants that are close to *Q. toumeyi*]; 10.3 km W of Restaurant Puerto de la Cruz, 11.6 km E of Santa Ana road on Mex 16, 28°22'19" N, 109°04'58" W, 1380 m elev., 31 Mar 1997, *Reina G. 97-462 with Van Devender* (NMC) [leaves proportionately narrow (3.1:1) like many *Q. toumeyi*, but with spirally contorted hairs].

Specimens intermediate between *Quercus barrancana* and *Q. oblongifolia*

CHIHUAHUA. Mpio. de Temósachic: 14 km E of Sonora border, 28°27' N, 106°26' W, elev. 1645 m., 23 Jun 1989, *Spellenberg, Boecklen, & Zimmerman 9853* (ARIZ, MEXU, NMC, TEX)

[leaves oval and relatively large for *Q. barrancana*, entire, but with glandular vermiform hairs and sparse, scattered crumpled multi-branched hairs]. **SONORA.** Mpio de Yécora: rock near Los Llanitos, elev. 1600 m, 18 Mar 1992, *Martin et al. s.n.* (ARIZ) [leaves oval or ellipsoid, entire, relatively large], 22 km W of Yecora on Mex. Hwy. 16, 8 km W of Puerto de la Cruz, 28°51'28.6" N, 109°04'58.8" W, 2117 m elev., 26 Apr 2005, *Spellenberg & Herrick 13512* (MEXU, NMC, NY, USON) leaves slightly obovate or oblong, very few branched hairs, margins entire].

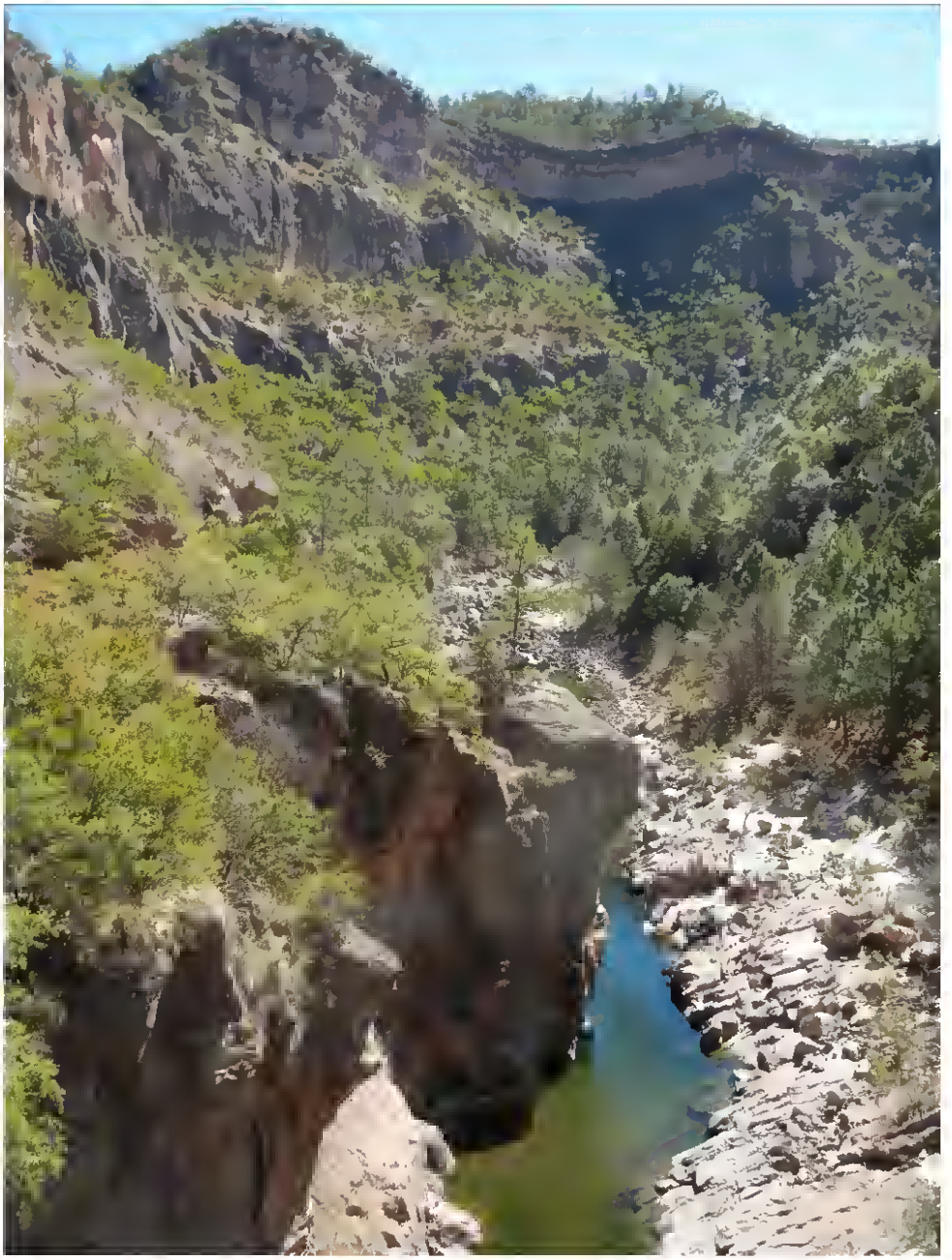

Figure 1. Habitat of *Quercus barrancana* along the Rio Urique, looking upstream from the Creel – Guachochi highway bridge. The oak forms the yellowish green vegetation on the SW-facing slope on left of photograph. Trees are bearing new spring leaves (photo 8 Mar 2012).

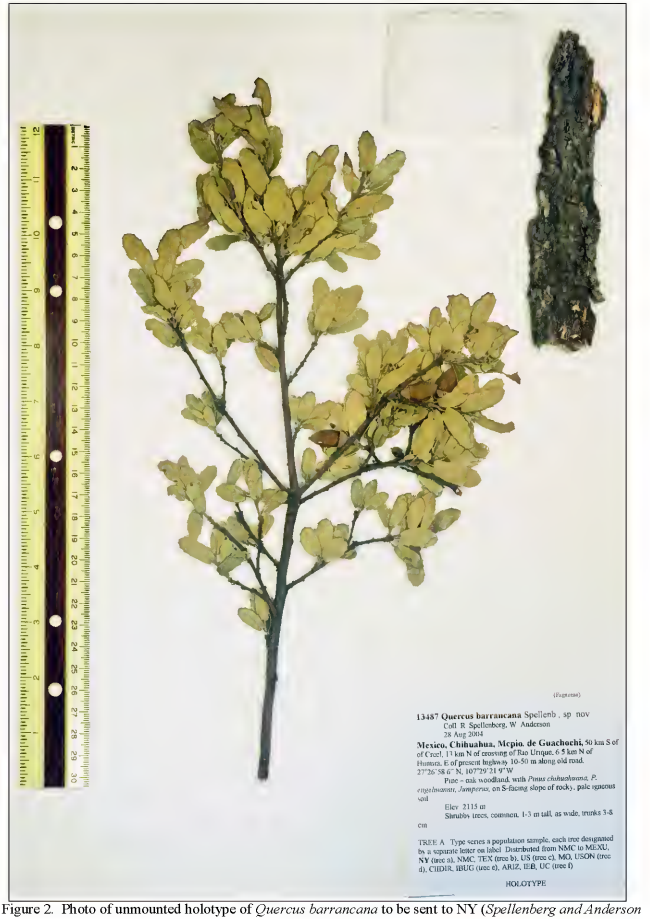

Figure 2. Photo of unmounted holotype of *Quercus barrancana* to be sent to NY (*Spellenberg and Anderson 13487*).

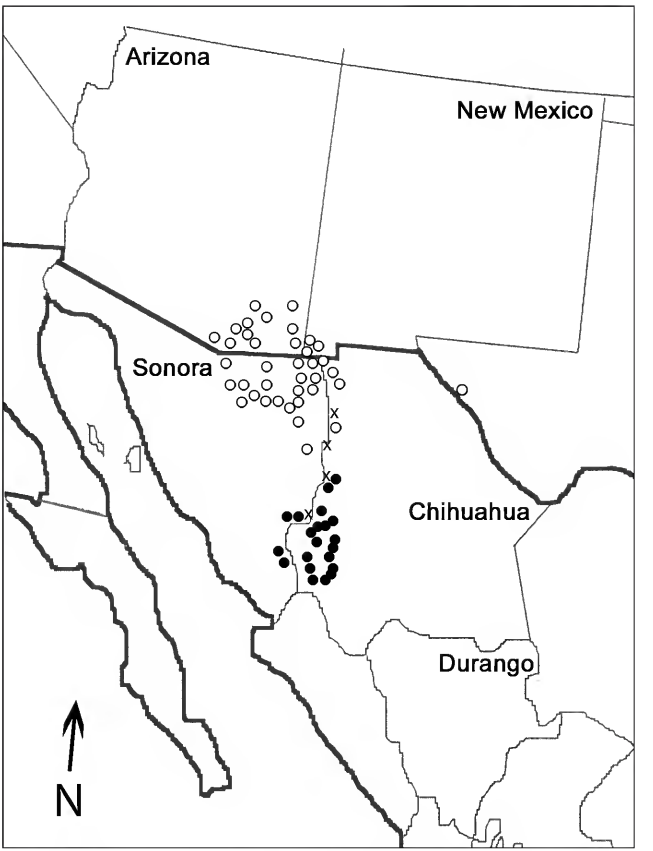

Figure 3. Map of distribution of *Quercus barrancana* and *Q. toumeyi* in southwestern USA and northwestern Mexico. Closed circles = *Q. barrancana*, open circles = *Q. toumeyi*, × = intermediate specimens between the species. See discussion in the section "Geographic Range" regarding *Q. toumeyi* in Texas.

Figure 4. Habit and habitat of *Quercus barrancana*. Trees are about 3-5 m tall, growing on thin soil over igneous rock along the Rio Urique, Chihuahua (photo 8 Mar 2012).

Figure 5. Leaves of *Quercus barrancana*, showing the characteristic broad, slightly obovate shape, toothed margins, and dark green mature color. (Photo 23 Sep 2012, at the type locality, courtesy of Wynn Anderson)

Figure 6. Variation in leaf size and shape within a population of *Quercus barrancana*. Each of the twigs on the specimen is from a different tree. Population is located about 10 km N of type locality (*Spellenberg and Zimmerman 8600*). Herbarium specimens from trees with leaves similar to those on twig at lower left were occasionally identified as being introgressed with *Q. arizonica*.

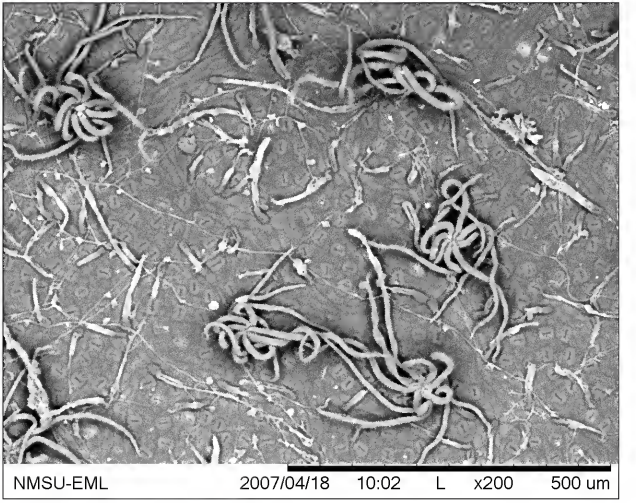

Figure 7. Scanning electron micrograph of abaxial surface of leaf of *Quercus barrancana* showing spirally contorted multirayed hairs, and smaller unbranched vermiform hairs. Leaf was collected in 2006 from a plant in type population, fixed in FAA (formalin, 95% ethanol, acetic acid, 2:1:1), stored in 70% ethanol, and viewed with a Hitachi TM-1000 scanning electron microscope.

Figure 8. An acorn of *Quercus barrancana* from the holotype. Distance from the tip of the nut to the edge of the involucre is 14 mm. Photo also shows slightly obovate, marginally toothed leaves, with paler abaxial surfaces.

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TYPIFICATIONS AND A NOMENCLATURAL CHANGE IN SOME EASTERN NORTH AMERICAN *OPUNTIA* (CACTACEAE)

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ABSTRACT

Recent advances in our understanding of the evolutionary relationships of eastern North American *Opuntia* closely allied to *Opuntia humifusa*, i.e., the *O. humifusa* complex, have resulted in the necessity for a taxonomic revision of the group. Here I neotypify two species described by Rafinesque for which no type specimens exist, *O. cespitosa* and *O. mesacantha*. I also change the taxonomic status of a species described by J.K. Small, *O. lata*, to subspecific rank, with the new combination **O. mesacantha** subsp. **lata** (Small) Majure **comb. et stat. nov**. *Opuntia macrartha* Gibbes also is neotypified based on material collected by J.K. Small from around the type locality for that taxon, as is *O. atrocapensis*, for which no type has ever been located.

Members of the *Opuntia humifusa* complex, primarily of eastern North America east of the Mississippi River, have been included in numerous treatments (Britton & Rose 1920, 1923; Small 1903, 1913, 1919, 1933; Radford et al. 1968; Benson 1981; Doyle 1990; Pinkava 2003; Wunderlin & Hansen 2011). However, there still are specific taxa within the group that have not been typified (e.g., *O. cespitosa* Raf., *O. mesacantha* Raf.; Rafinesque 1830) or for which the type specimens no longer exist (e.g., *O. macrartha* Gibbes) or have never been found (*O. atrocapensis* Small; see Benson 1982). This group is the subject of a taxonomic revision (Majure et al. in prep.) and has been studied in detail from a phylogenetic as well as morphological and cytogenetic standpoint (Majure & Ervin 2008; Majure & Ribbens 2012; Majure et al. 2012a & b, 2013; Majure et al. in prep.). These recent studies also have provided evidence for the recognition of subspecific taxa of two distinct ploidal levels (diploid and tetraploid; Majure et al. 2012b; Majure et al. in prep.) within the more widespread species, *O. mesacantha*. That nomenclatural change is also provided below.

Opuntia atrocapensis Small, Man. SE. Fl. 905. 1933. **TYPE**: not found. **NEOTYPE** (designated here): **USA. Florida.** Monroe Co.: sand dunes; Middle Cape Sable, 28 Nov 1916, *J.K. Small s.n.* (US!).

Opuntia cespitosa Raf., Bull. Bot. Seringe. 216. 1830. **TYPE**: not designated by the author. **NEOTYPE** (designated here): **USA. Kentucky.** Woodford Co.: Hwy 60 N at jct. of Hwy 62, just N of Versailles, 9 Jun 2008, *L.C. Majure 3275* (neotype: FLAS!; isoneotype: US!). Note: the specific epithet for this taxon is often spelled "*caespitosa*;" Rafinesque (1830), however, first published the name as "*cespitosa*," so that spelling is maintained here. Non *Opuntia caespitosa* Poepp., Reise Chile 356. 1835.

Opuntia mesacantha Raf. Bull. Bot. Seringe. 216. 1830. **TYPE**: not designated by the author. **NEOTYPE** (designated here): **USA. Virginia.** Hampton, 31 May 1878, *J.W. Chickering, Jr. s.n.* (US!).

Opuntia mesacantha subsp. ***lata*** (Small) Majure, **comb. et stat. nov.** *Opuntia lata* Small, Jour. N. Y. Bot. Gard. 1919. **TYPE**: **USA. Florida.** [Alachua Co.], pine-woods, 12 mi W of Gainesville, 13 Dec 1917, *J.K. Small s.n.* (holotype: NY!).

Opuntia macrartha Gibbes, Proc. Elliott Soc. Nat. Hist. 1: 273. 1859. **TYPE: USA. South Carolina.** within a few miles of Charleston, [1 Sept 1857, presumably collected by Gibbes], no repository cited. Gibbes' collection was housed at, and subsequently disappeared from, the Charleston Museum during the US Civil War (see Benson 1982). **NEOTYPE** (designated here): **USA. South Carolina.** Charleston Co.: Isle of Palms, near Charleston, 14 Feb 1916, *J.K. Small s.n.* (neotype: US!; isoneotypes: NY! US!).

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ANOTHER REVIEW OF THE *SYMPHYOTRICHUM PATENS* COMPLEX (ASTERACEAE), INCLUDING A NEW VARIETY OF *S. PATENS* FROM THE SOUTHERN BLACKLANDS, NEW RECORDS OF *S. GEORGIANUM*, AND NOTES ON *GEORGIANUM*-LIKE PLANTS OUTSIDE ITS KNOWN RANGE

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ABSTRACT

Taxonomy of the *Symphyotrichum patens* complex (*S. patens*, *S. phlogifolium*, *S. georgianum*) is reviewed and a new variety is described: **S. patens** var. **terranigrum** Campbell & Seymour. This variety is known mostly from the Black Belt grasslands of Alabama and Mississippi, but it extends east to calcareous soils on the Piedmont of North Carolina. Also, there are a few records of similar plants from the southern Interior Low Plateaus and the Ridge and Valley region as far north as Pennsylvania. Var. *terranigrum* is distinct in the minute stipitate glands on stems and leaves, with non-glandular hairs dense or sparse or absent. In most variants of *S. patens*, glands are largely restricted to involucres and non-glandular hairs are dense, although glands are widespread in some plants of more typical *S. patens* that are concentrated in Appalachian regions. Leaves of the new variety tend to have a bluish-waxy sheen, usually darkening when dried; mid-stem leaves tend to be relatively short and clustered; and bracteal leaves tend to be abuptly reduced above the peduncle base. However, several collections appear transitional to var. *gracile* or var. *patens*. It is suggested that the presence of glands on stems and leaves is ancestral within the complex and that var. *terranigrum* partly corresponds to the diploid population mapped by previous authors in the Black Belt. A hypothesis is proposed: that dense stipitate glands in these plants contribute to deterrence of herbivores, which have generally been a stronger selective force on more base-rich soils due to promotion of herbivory by productive nutritious vegetation. Among taxa of *Symphyotrichum* subg. *Virgulus* sect. *Patentes* plus sect. *Grandiflori* (sensu lato), glandularity appears to be associated with preference for base-rich soils. The polyploid *S. georgianum*, with distinct rhizomes and unusually large flowering heads, is partly allopatric with the other two species. It is concentrated in medium acid to base-rich grasslands and thin woodlands on or near the Piedmont. However, there is significant variation in habit and glandularity in *S. georgianum*, together with similar plants from Texas to Pennsylvania. New county records are provided for *S. georgianum*, including the first from Tennessee. A largely eglandular variant of *S. georgianum* is concentrated on the Atlantic Coastal Plain. An undescribed *georgianum*-like taxon could be based on distinct collections concentrated in Texas and ranging from Oklahoma to Georgia. In contrast to typical *S. georgianum*, these plants usually produce shorter rhizomes or offsets (<15 cm long), and shorter stems (mostly 20–60 cm vs. 50–100 cm). Their leaves are usually eglandular, and those below mid-stem are sometimes relatively large and more persistent to flowering. Their inflorescences tend to be less widely branched, with smaller heads. But the inflorescences of both typical *georgianum* and these "short western" plants are usually distinct from other taxa of the *S. patens* complex in their somewhat compact form with ascending branches. Observations of cultivated plants and cytological investigation of these apparent variants or allies of *S. georgianum* would be useful for a better understanding of the whole complex.

Like violets in spring, the North American asters now known as species of *Symphyotrichum* sometimes seem designed to provoke exasperation and discord amongst systematic botanists during autumn, whilst the general public admires them from a more relaxed aesthetic perspective. Subgenus *Virgulus* (Raf.) Nesom is a relatively distinct and showy division within the genus; it is characterized by rays usually blue to purple, phyllaries usually stipitate-glandular, cauline leaves 3-nerved, rounded to auriculate or amplexicaul at sessile bases, and a basic chromosome number of x = 5. But concepts of appropriate sections within subg. *Virgulus* remain unsettled, from A. Jones (1980) to Brouillet et al. (2006). Moreover, among plants known as sect. *Patentes* (Torr. & Gray) Nesom the circumscription of some taxa and their relationships remain uncertain.

Based on Brouillet et al. (2006), the core of sect. *Patentes* comprises *Symphyotrichum patens* (Ait.) Nesom, *S. phlogifolium* (Muhl. ex Willd.) Nesom, and *S. georgianum* (Alex.) Nesom. In addition, *S. adnatum* (Nutt.) Nesom and *S. walteri* (Alex.) Nesom could be included, but those species of southeastern sandhills and pine flatwoods are highly distinctive in their somewhat scandent habit and in their adnate viscid distal leaves (*adnatum*) or somewhat succulent leaves (*walteri*). Two additional species also appear relatively close.

(1) *S. novae-angliae* (L.) Nesom is a widespread robust weedy species of relatively fertile soils in eastern states: diploid (2n = 10) or rarely tetraploid (A. Jones 1980; Semple 1984), with unusually large heads that have somewhat foliaceous, densely glandular phyllaries, and relatively narrow leaves (length/width ca. 5–10 versus 2.5–5) that are unusually dense up into lower parts of the somewhat corymbiform inflorescence. It has been considered the sole member of sect. *Polyliguli* but it could be grouped with the following.

(2) *S. grandiflorum* (L.) Nesom is restricted to the Carolinas and Virginia, especially on sandy soils: dodecaploid (2n = 60) or occasionally hexaploid (Brouillet et al. 2006), with spreading rhizomes, more cuneate distal leaves and scabrous phyllaries. It has been grouped in sect. *Grandiflori* with some widely scattered diploid species that have less auriculate-clasping leaves: *S. campestre, S. pygmaeum, S. yukonense, S. fendleri* and *S. oblongifolium*.

It is likely that all of these species (listed in this paragraph) form a largely monopyletic group, distinguished from sect. *Virgulus* plus sect. *Ericoidi* by the presence of stipitate glands, at least in the inflorescence. However, there has probably been some reticulate evolution, as illustrated by *S.* × *amethystinum*, a common hybrid of *S. novae-angliae* and *S. ericoides* (Chmielewski & Semple 2003).

Symphyotrichum patens, *S. phlogifolium*, and *S. georgianum* are species of southeastern states (Figure 1) that have been the focus of studies by R. Jones (1980, 1983, 1992). *Symphyotrichum phlogifolium* is a tetraploid (2n = 20) centered in Appalachian regions and typical of relatively mesic, shady habitats. It has often been confused with *S. patens*, which is a widespread southeastern species that occurs mostly in more dry and open habitats. *Symphyotrichum georgianum* is a generally distinctive decaploid (2n = 50) of dry woodlands and grasslands in a restricted southeastern range (Brouillet et al. 2006). These three species share phyllaries that are unequal and non-foliaceous, pubescent at least on margins, their apices green and usually somewhat glandular but not densely so (less than *novae-angliae*). Both proximal and distal cauline leaves generally have somewhat auriculate or amplexicaul bases, although this character is often less obvious along inflorescence branches, where leaves are usually much reduced.

Nesom (2006) reviewed the mapping of chromosome numbers in *Symphyotrichum patens* by R. Jones (1980, 1983), Semple (1984), and others. He confirmed that tetraploids are widespread across southeastern states but that diploids (2n = 10) are concentrated on the Gulf Coastal Plain. Although diploids have generally not been recognized as distinct taxa, initial crossing experiments have indicated that significant barriers to pollination exist between diploids and tetraploids (Jones 1983). One cluster of recorded diploids occurs in or near the Black Belt of Mississippi and Alabama.

R. Jones (1980) had previously noted somewhat distinctive plants in the Black Belt, especially among diploids with "strongly adnate-ascending leaves and peduncular bracts, heavy glandular pubescence, and larger involucres." However, he found that these characters also occurred to some extent within tetraploids from that region and decided not to describe a new taxon. Some diploids west of the Mississippi River have been assigned to var. *gracile* (Hook.) Nesom by Jones (1983) and Brouillet et al. (2006). But Nesom (2006) reassessed var. *gracile* and could not discern a "geographic zone of morphological discontinuity that would enable or justify the recognition of two taxa." He concluded that only one additional variety is clearly distinguishable from typical *S. patens* var. *patentissimum* (Lindl.) Nesom, which comprises tetraploids centered in the Ozarkian region.

The initial impetus for this paper was the observation of distinctive *patens*-like plants during 2009 at the Pulliam Prairie (Chickasaw County, Mississippi), which is one of the best known remnants of native grassland in the Black Belt (Campbell & Seymour 2011a, 2011b, 2012). These plants appeared to match R. Jones's (1980) description of diploids in the Black Belt. Subsequently, the first author reviewed collections filed under *Symphyotrichum patens* at several herbaria across southeastern states, to see if a new taxon was worth recognizing, and if so, how distinctive it might be and where it occurs. During this review, many collections in the *patens-phlogifolium-georgianum* group were examined, and deeper complexity was discovered among *georgianum*-like plants than has been previously described. These observations are summarized below in the form of a provisional key, plus notes on individual taxa and selected maps.

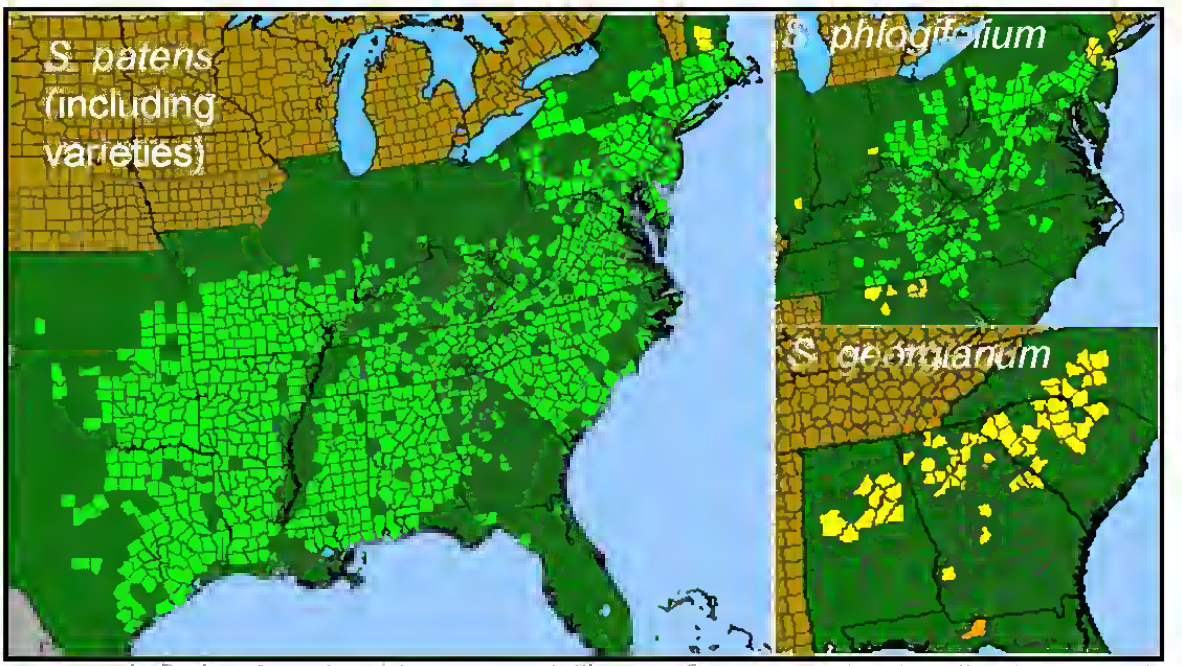

Figure 1. Distribution of *Symphyotrichum patens* and allies according to Kartesz (2014). Yellow (versus green) county shading indicates official rare status within the state. Note that records of *S. phlogifolium* from Illinois (USDA 2014a) and Mississippi (Cronquist 1980) remain unverified, and that some intergradation with *S. patens* may occur across its range. Also, *S. georgianum* has been reported from Louisiana (R. Jones 1980, 1983), and various *georgianum*-like collections exist that may extend the range of this species, see notes in text below.

A new variety of *Symphyotrichum patens* from the southern Blacklands

SYMPHYOTRICHUM PATENS (Ait.) Nesom var. **TERRANIGRUM** J.J.N. Campbell & Seymour, **var. nov.** Figures 2, 3. **TYPE: USA. Mississippi.** Chickasaw Co.: Pulliam Prairie, locally common in dry grassland on chalk, 24 Sep 2009, *W.R. Seymour & J.J.N. Campbell *483* (holotype: MISS; isotype: APSC). Paratypes from same population, 23 Aug 2009, *Seymour & Campbell *482a* [few hairs] & *482b* [denser hairs] (MISS, APSC).

Similar to *Symphyotrichum patens* var *gracile* (Hook.) Nesom but differing in the dense to sparse stipitate glands on leaves and stems and in the mid-stem leaves (directly below inflorescence) with length/width (1.5–)2–2.5(–3), clustered and overlapping along 10–20 cm.

Perennial herbs usually 40–80 cm tall, cespitose, with short thick woody caudices and no rhizomes. **Stems** 1–5+, ascending to erect, with minute stipitate glands densely to sparsely scattered from peduncle to base, longer non-glandular hairs dense, sparse or largely absent. **Leaves** usually with bluish-waxy sheen and blackening when dried, relatively thick and stiff, with minute stipitate glands dense (especially on petioles and midribs) to sparse, otherwise glabrous to scabrid-puberulent with non-glandular hairs. **Lower leaves** early deciduous, subpetiolate with distinct constriction above flared base, blades spatulate to obovate, mostly 3–6 × 1.2–2.6 cm, bases cuneate, margins entire or subentire, apices acute to rounded. **Mid-stem leaves** (below peduncular branches) usually clustered on 10–20 cm of stem, with internodes as short as 4–10 mm, sessile, blades ovate to lanceolate, (2–)3–5(–7) × (0.8–)1.1–2.3(–2.5) cm, with length/width = (1.5–)2–2.5(–3), their bases strongly cordate-clasping to slightly auriculate, apices acute to rounded. **Distal leaves** (along peduncular branches) distinctly reduced up each branch order, sessile, blades broadly to narrowly ovate, mostly 1–3 × 0.5–2 cm, bases strongly cordate-clasping to auriculate-amplexicaul, apices usually acute. **Heads** mostly 2.5–3 cm wide, in paniculiform arrays with divaricate branches. **Peduncles** stiffly ascending, slender, up to 3–9 cm long, bracts appressed to spreading, linear, lowest ones mostly 7–9 × 2–3 mm, abruptly reduced along peduncle to 0.3–2 mm wide, grading into phyllaries. **Involucres** campanulate, ca. 6–9 mm. **Phyllaries** in 5–7 unequal series, appressed to slightly squarrose, lanceolate to linear, ca. 4.5–6.5 × 1–1.5 mm, bases ± indurate in proximal third, margins hyaline, erose to ciliolate distally, green zones diamond-shaped in distal third, outer apices obtuse to acuminate, inner apices often purplish red, faces strigillose to puberulent abaxially and near tip adaxially, stipitate-glandular distally. **Ray florets** ca. 15–30; corollas light violet, laminae ca. 6–12 × 1–2 mm. **Disc florets** ca. 25–50; corollas yellow, ca. 5–6 mm, tubes shorter than narrowly funnelform throats, lobes triangular, ca. 0.5 mm. **Cypselae** dull brown to purplish, oblong-obovoid, ca. 1-1.5 mm, faintly 5–8-nerved, faces white-sericeous, especially on nerves; pappi tawny, ca. 4-5 mm.

Flowering September to October. Blackland prairies, calcareous glades, associated roadsides and woodland edges. Alabama, Georgia, Mississippi, New York, North Carolina, Pennsylvania, North Carolina, South Carolina, Tennessee, Texas, West Virginia (Figure 4).

Additional collections examined are as follows; acronyms for herbaria follow Thiers (2014). In most plants, stipitate glands and regular non-glandular hairs are both more or less densely scattered over leaves and stems, but these characters often vary within populations. Collections with asterisks (* before herbarium acronyms) have stipitate glands but much sparser regular hairs. Collections with question marks (? before herbarium acronyms) have few glands and appear somewhat transitional from var. *terranigrum* to var. *gracile* or to var. *patens*.

USA. Alabama. Autauga Co.: in fairly moist prairie clay in full sun, Jones Bluff, W shore of Alabama River ca. 4 mi N of Jones Bluff Dam, SSE of Statesville, T16N R13E Sec. 8, 18 Aug 1982, *Gunn 1090* (?VDB). Bibb Co.: ca. 5.5 mi S of Centreville/Brent, powerline and roadside ketona dolomite glade at junction Highways 5 and 219, T24N R6W Sec. 26 SE/4, 2 Nov 1996, *MacDonald*

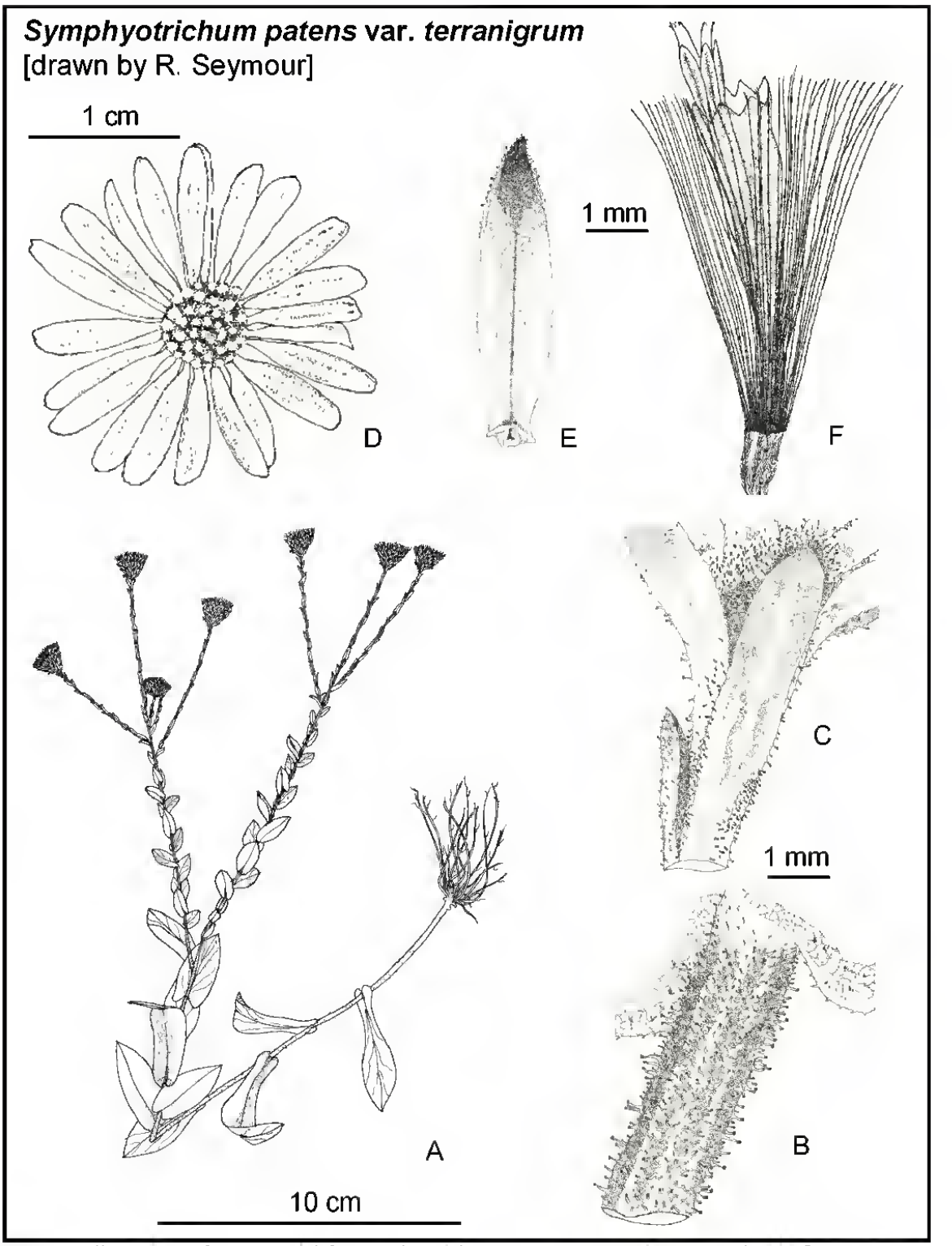

Figure 2. Illustrations of type material for *Symphyotrichum patens* var. *terranigrum*. A. Plant in flower. B. Stem, middle section. C. Stem, summit below involucre. D. Flowering head from above. E. Involucral bract. F. Fruit (cypsela), floret, and pappus.

9984 (IBE, MISS, MMNS); ca. 9.2 mi NE of Centreville, ca. 0.8 mi W of Bulldog Bend Bridge, "Goat Glade South," Ketona Dolomite outcrop above right (W) bank of Little Cahaba River, 8 Oct 2000, *Allison 12566* (UNA). Colbert Co.: dry calcareous glady place ca. 1 mi SW of Littleville, 30 Sep 1952, *Harper 4218* (?MO, ?NCU, ?UNA, US, "*Aster tenuicaulis*"). Crenshaw Co.: Ala. Hwy 95 ca. 1 mi S of County Hwy 19, black belt roadside, full sun, dry chalk soil, 29 Oct 1995, *Diamond 10087* (BRIT); dirt roadside 0.3 mi N of Briar Branch, sandy clay soil, full sun, common, T10N R17E Sec. 8, 14 Oct 2001, *Diamond 12784* (*BRIT). Hale Co.: prairie edge by county [road] 61 ca 9.5 mi N of Uniontown, 6 Oct 1972, *Kral 48849* (?BRIT, MO, TENN, "*Aster patens* Ait. var."). Lawrence Co.: sandy clay of oak-pine hills by Ala 33 8.8 mi S of Moulton, 23 Sep 1970, *Kral 41252* (MO). Madison Co.: "monte near Huntsville, northern district," 27 Oct 1887, *Mohr s.n.* (UNA). Marengo Co.: ca. 3 mi S of Demopolis along US 43, outcrop of Demopolis Chalk, 7 Oct 1967, *Kral 29633A* (BRIT, VDB); chalk glades on W side of Demopolis by US 80, 6 Oct 1972, *Kral 48872* (MO, TENN, ?VDB, glands sparse, leaves rather large). Shelby Co.: Oak Mountain Park, ridge near Peavine Falls, sunny, sandy-loam, dry area, infrequent, 23 Nov 1962, *Deramus 239* (UNA). Sumter Co.: 1 mi N of Epes, soft chalk outcrop, strongly caespitose, infrequent, 12 Sep 1967, *Thomas 1211* (*NCU, *UNA); chalk prairie edge above Tombigbee River just N of Epes, 5 Oct 1972, *Kral 48759* (*MO, *TENN, VDB, "*Aster patens* Ait. var. ?"); chalk barrens between Gainesville and Geiger by Ala. 116, 19 Sep 1975, *Kral 56580* (VDB); Rte. 116 2.6 mi W of jct with Ala. 39, chalk outcrops, 7 Nov 1977, *R. Jones 2123* (VDB); US 11 at Tombigbee River, chalk outcrops, 8 Nov 1977, *Jones 2141* (*VDB); chalky soil beside I-59 and I-20 about 0.7 mi S of the Epes Exit on Ala. 21, S of Tombigbee River, 31 Oct 1993, *Thomas & Thomas 138,487* (*TENN); 0.3 air mi NW Old Bluffport, chalk outcrop, 32-35-37 N, 88-03-39W, 24 Oct 2006, *Keener 3260* (?UNA). **Georgia**. Bibb Co.: growing in a pine-hardwood site 1-1.2 mi S of junction of Montpelier Station Rd and Hwy 74 W on the Payne Property, 30 Sep 1991, *J. & R. Payne s.n.* (GA). Catoosa Co.: in a grassy road edge on Lovingood Road, *DeSelm s.n.*, 3 Oct 1987 (EKY). Floyd Co.: Coosa Prairie, 20 Jun 2010, *Medley et al. s.n.* (in prep.). **Louisiana**. St. Tammany Pa.: Covington, 31 Oct 1919, *Fr. Paul 1223* (?BRIT, glands sparse, leaves not much reduced or crowded; collector perhaps Abbot Paul Schauble, head of Benedictine Order in Louisiana ca. 1910). **Mississippi**. Lauderdale Co.: sandy cut-over wooded hill 0.4 mi W of Alabama line and E of Lauderdale, 24 Sep 1966, *Jones 10624* (*MISS). Neshoba Co.: open field and edge of ditch, State Highway 15, 9.5 mi S of Williamsville, 30 Sep 1967, *Temple 7492* (BRIT, GA, MISS); open field and edge of ditch on St Hwy 15 2.1 mi S of Lynwood, 12 Oct 1968, *Temple 10924*. Oktibbeha Co.: Rock Hill, steep N-facing bluff and associated chalk barrens ca 6 mi N of Starkville along Trim Cane Creek, 20 Oct 1930, *Gordon & Jones 3040* (?MMNS, perhaps closer to var. *gracile*); T19N R15E Sec. 16 on Old West Point Rd just E of railroad tracks, chalk outcrops on S side of road, 11 Sep 1994, *Leidolf 0932* (VDB, IBE); T19N R15E Sec. 16 SW/4, Osbourne Prairie, 0.25 mi N of Old West Point Rd and 16th Sect Rd, on 16th Section Rd, E of 16th Section Church cemetary and transmission lines, open chalk barrens bordered by Black Belt prairie, 14 Oct 2003, *Sullivan et al. 03-299* (*MMNS, depauperate); 16th Section Prairie, 26 Sep 2004, *Fishbein 5463* (?MISSA, perhaps closer to var. *gracile*). Walhall Co.: dry upland R/W State Highway 48 just W of Walthall-Marion Co. line, 4 Sep 1970, *Temple 12654* (?MISS). **New York**. Nassau Co.: Hemstead Plains, Long Island,16 Sep 1893, "*The Jos. Schrenk Herb. presented 1902*" (?MO, see notes in Discussion). **North Carolina**. Graham Co.: edge of woods along Yellow Creek, near Lake Fontana, 30 Sep 1995, *McNeilus 95-579* (MISSA-Entomology, TENN, "*Aster patens* var. *georgianus*," depauperate collection). Onslow Co.: flat pine-oak woods 0.6 mi NNW of Silverdale on road to Belgrade, 4 Oct 1957, *Ahles 36015* (NCU). Orange Co.: roadside near upper bridge, Morgan Creek, 3 Oct 1909, *Coker s.n.* (NCU); dry soil in open woods Duke Forest, 25 Sep 1932, *Blomquist 5084* (WVU). **Pennsylvania**. Lehigh Co.: open grassy place beside road at crest of wooded slope along stream, ca. 1.75 miles NNW of Emaus Post Office, 14 Oct 1917, *Pretz 9204* (NCU). **South Carolina**. Aiken Co.: "Aiken", 28 Sep 1866, *Ravenel s.n.* (MO). Chester Co.: clay margin of cutover pine woods near Armenia Church ca. 10 mi SSW of Chester, 18 Sep 1957, *Bell 10083* (?NCU). Lexington Co.: infrequent at edge of dry woods on crest, powerline row next to subdivision on N side Six Mile

Creek, E of US 321, Cayce, 29 Sep 1988, *Nelson 7064* (USCH). York Co.: scattered with *Sporobolus clandestinus* on hard thin soil (Iredell) over gabbro, S side of Locust Hill Rd (= S-63) near junction with S-75, W of York, 27 Oct 1988, *Nelson 7181* (USCH). **Tennessee**. Maury Co.: glade area SE of Columbia between highways 50 and 50A, 3 Oct 1979, *Collins 4582* (VDB, unusually narrow leaves). Rutherford Co.: rise in limestone prairie by US 41, SE side of Luverne, 24 Sep 1979, *Kral 64381* (?VDB); glades and barrens along Chaney Rd just off jct. with San Ridley Parkway at I-24, 16 Oct. 1984, *McKinney 01605* (VDB, primary branches with oblong leaves); Flat Rock State Natural Area, inside firelines ca. 0.5 trail-miles from Factory Road, 20 Sep 2007, *McCoy & Crabtree s.n.* (?APSC). Sullivan Co.: rocky roadside bank on Mt. City-Bristol Rd., 13 Oct 1940, *Shanks 1131* (MISS) and *Sharp 1133* (TENN). **Texas**. Brazos Co.: 1 mi W of College Station, ungrazed field with *Andropogon scoparius*, 7 Oct 1949, *Swank s.n.* (?WVU). Harris Co.: dry prairie near Houston, middle of June 1843, *Lindheimer s.n.* (?BRIT, "*Aster patens* var.", glands few and mostly on small bracts of infl. branches, but leaves dark and crowded); Houston, prairies, 18 Sep 1917, *Palmer 12785a* (MO, "*Aster tenuicaulis*"). **West Virginia**. Jackson Co.: common, dry roadbank on ridgetop, Co Rt 19 at Hickory Chapel, 2.25 mi E Rt I-77 and W of Kentuck, 11 Oct 2000, *Cusick 35693* (MU). Pendleton Co.: US-220 3.1 mi N of Franklin on US-33, 9 Oct 1981, *Semple & Chmelewski 5893* (MO, "*Aster phlogifolius*... 2n = 20 from rootstocks").

Most records of more distinctive plants are from the Black Belt on Cretaceous chalk in Alabama and Mississippi, but this taxon does extend east onto strips of calcareous soil along the Piedmont and Coastal Plain as far as North Carolina, and there is at least one distinctive collection from Texas (*Palmer 12785a*). There are also a few collections that appear at least transitional to this new variety from the southern Interior Low Plateaus in Alabama and Tennessee, and from the Ridge-and-Valley region as far north as Pennsylvania. At the Pulliam Prairie, *Symphyotrichum patens* var. *terranigrum* grows in xeric to xerohydric grassland on gently sloping uplands with clayey vertisols derived mostly from Cretaceous chalk (Campbell & Seymour 2011b, 2012). The most common graminoids include *Aristida longespica*, *Sporobolus vaginiflorus***, *S. clandestinus**, *S. compositus* var. *drummondii**, *Schizachyrium scoparium*, *Panicum flexile**, *P. virgatum**, *Carex crawei***, *C. meadii***, and *Sisyrinchium albidum***. Locally frequent herbs include *Agalinis gattingeri**, *A. oligophylla***, *Asclepias viridiflora***, *Coreopsis lanceolata*, *Dalea candida***, *D. purpurea***, *Erigeron strigosus* var. *calcicola***, *Eurybia hemispherica**, *Houstonia lanceolata**, *H. nigricans***, *Hypericum sphaerocarpon***, *Liatris squarrosa* var. *glabrata***, *Linum sulcatum***, *Lobelia spicata* var. *leptostachya***, *Ruellia* cf. *humilis***, *Spiranthes magnicamporum***, *Solidago nemoralis*, and *Symphyotrichum laeve* var. *purpuratum**. Typical woody species in the intermixed thickets and woodland edges include *Berchemia scandens*, *Celtis tenuifolia***, *Cercis canadensis**, Cornus drummondii**, *Crataegus crus-galli** [sensu lato], *Fraxinus americana** [sensu lato], *Juniperus virginiana**, *Maclura pomifera***, *Prunus angustifolia**, *Sideroxyon lycioides***, and *Rhus glabra**. *Quercus stellata* and *Q. marilandica* are locally abundant in adjacent woodland on ridges and knolls at slightly higher elevation. [* Asterisks here indicate species more common on base-rich soils; double asterisks indicate strong concentration; these allow easy comparison with other taxa below.]

Var. *terranigrum* varies considerably in the density of glands versus non-glandular hairs and in other characters, as noted above under the list of collections. At the Pulliam Prairie, plants more similar to var. *gracile* occur locally in the thin oak woods and edges on more acid clayey soils that overlie the characteristic chalk of the Black Belt. Some of the variation within this extensive remnant of the original vegetation, and at other sites, might be interpreted as intergradation between the varieties. Nevertheless, var. *terranigrum* is a generally distinctive, locally frequent plant in the Black Belt grasslands, and it deserves to be studied in more detail across southeastern states. Plants with dense glands but little or no pubescence on leaves and stems may be the 'purest' examples of var. *terranigrum*, known only from a few sites in the Black Belt of Alabama (Crenshaw and Sumter cos.) and Mississippi (Chickasaw, Lauderdale, and Oktibbeha cos.); see annotated list of collections above.

Symphyotrichum patens var. *terranigrum* is named after the 'blacklands' of southeastern states, which are concentrated on the Gulf Coastal Plain. The sticky 'xerohydric' vertisols of these regions form typical habitat for the plant (Campbell & Seymour 2011a). This taxon does not appear to have been recognized by earlier authors, but the history of varietal names within *S. patens* still needs clarification (Jones 1983; Nesom 2006). R.N. Harper in Alabama and E.J. Palmer in Texas both applied the name *Aster tenuicaulis* (C. Mohr) Burgess (in Small 1903) to their collections of var. *terranigrum*. However, Mohr (1901) had named "*Aster patens tenuicaulis*" for plants from sandy soils in southern Alabama (Washington and Mobile cos.) in order to replace "*Aster patens gracilis*" of Hooker (1835), which was based on a type from Louisiana (Jacksonville Springs in Washington Parish) — not from Florida as assumed by Mohr. The appropriate treatment for "*Aster gracilis*" of Nuttall (1818) remains uncertain, since it was originally recognized "in the savannahs of Kentucky and Tennessee" — indicating typical *S. patens* — and Nuttall's description (with leaves "subamplexicaule") also suggests that he was referring at least in part to typical *S. patens*. Yet Asa Gray and others have identified a type collection for *A. gracilis* Nutt. as the plant now known as *Eurybia compacta* Nesom (Nesom 1995).

Figures 3a-g [with next pages]. *Symphyotrichum patens* var. *terranigrum* at Pulliam Prairie in 2009.
(a) Whole plant [above].
(b) Mid-cauline leaves, showing relatively short clustered leaves.
(c) Upper cauline leaves, below branching of inflorescence.
(d) Lower branching of inflorescence.
(e) Terminal view of inflorescence with minute peduncular bracts.
(f) Lateral view of head showing slightly squarrose phyllaries with darkened apices.
(g) Terminal view of head with maturing peripheral disc florets.

b (above) and c (below)

d (above) and e (below)

f (above) and g (below)

Provisional key to the *Symphyotrichum patens* complex

This synoptic key to *Symphyotrichum patens* and its allies has been modified from keys of Jones (1983), Brouillet et al. (2006), and Nesom (2006), after considerable trial and error in herbaria. But because some of these taxa — or potential taxa — will probably become circumscribed in more detail and adjusted, the key must still be regarded as provisional. Notes on problems with individual taxa are provided below.

1. Inflorescence usually somewhat compact (racemiform or corymbiform), at least in sections, with ascending branches; heads often up to 4–5 cm across, the ray laminae up to 14–24 × 1.5–3.5 mm, usually deep violet or purplish, the phyllaries mostly squarrose; mid-stem and distal leaves clasping to subclasping, usually widest near the middle; leaves usually somewhat waxy-thickened and deep bluish green, their areolae mostly 1–1.5 mm across, their margins often thickened, revolute and more or less undulate; rhizomes often produced.

2. Plants usually producing short offsets or rhizomes <15 cm long, 20–60 cm tall and drying to relatively pale olive/grayish-green; leaves usually eglandular; some leaves below mid-stem often distinctly larger and persistent to flowering; involucres mostly 6–8 mm high, the heads mostly 2.5–4 cm wide, up to ca. 15(–30) per stem in more or less corymbiform arrays ..... **Symphyotrichum** aff. **georgianum**, possible new taxon
[These are the "short western plants" noted below from Alabama, Georgia, Louisiana, Mississippi, Oklahoma, and Texas.]

2. Plants usually producing distinct rhizomes >15 cm long, 50–100 cm tall and often drying to relatively dark bluish-green; leaves with or without dense glands; leaves below mid-stem not especially large and generally withering before flowering; involucres mostly 8–12 mm high, the heads mostly 3–5 cm wide, up to to ca. 30(–60) per stem in more or less racemiform to paniculate arrays.

3. Stems and leaves glandular; heads mostly 4–5 cm wide ..... **Symphyotrichum georgianum**, glandular variant

3. Stems and leaves eglandular; heads mostly 3–4 cm wide ..... **Symphyotrichum georgianum**, eglandular variant

1. Inflorescence broad or somewhat elongated, but not distinctly compact with ascending branches; heads mostly 2.5–4 cm across, the ray laminae 9–18 × 1–3 mm, usually pale blue/lavendar to pale violet/purplish, the phyllaries appressed or squarrose; mid-stem and distal leaves strongly cordate-clasping, their bases almost as wide as their middles; leaves waxy-thickened and deep bluish-green (especially more glandular plants) or thin and paler yellowish-green, their areolae mostly 0.5–1 mm across, their margins flat or slightly thickened, not undulate; rhizomes usually lacking or indistinct.

4. Leaves thin, pliable (almost membranaceous), softly pubescent with long and short hairs, the secondary veins somewhat raised (rugose, wrinkled); larger mid-stem leaves mostly 8–13 × 2–3 cm, gradually narrowed in distal half to an acute apex; stems and leaves with dense stipitate glands in addition to hairs; peduncles mostly (0.5–)1–2(–3) cm long, the inflorescence usually no more than 20 cm wide and longer than wide; phyllaries in 3–4 unequal series, appressed, glandular; rays pale to dark purple (with slight reddish hue); disc corollas and pollen mostly white except for the ca. 1–1.5 mm lobes, which turn purple; cypselae ca. 2.5–4 mm, dark brown to black, with short hairs (ca. 0.2–0.3 mm) restricted to ribs ..... **Symphyotrichum phlogifolium**

4. Leaves thick, firm, usually short-hirsute to scabrous (sometimes almost glabrous), the veins not conspicuously raised; larger mid-stem leaves mostly 2–7 × 0.5–2.5 cm, narrowed in distal third to an acute or obtuse apex; stems and leaves with stipitate glands absent, scattered or dense; peduncles mostly 2–13 cm long, the inflorescence up to 30–50 cm wide, usually wider than long;

phyllaries in 4–7 strongly unequal series, appressed to squarrose, glandular to eglandular; rays usually pale blue to violet (sometimes lavendar to slightly purplish); disc corollas and pollen usually bright yellow [when fresh], including the ca. 0.5–1 mm lobes, or the lobes sometimes turning purple [especially in Appalachian plants]; cypselae ca. 2–3.5 mm, gray to brown, with long ascending hairs (ca. 0.4–0.6 mm) on and between ribs.

5. Involucres broadly turbinate, mostly 8–12 mm long; phyllaries in 4–7 series (grading into bracts), more or less appressed, obtuse to acute, middle ones 1.2–1.7 mm wide (ovate-lanceolate), densely strigillose or sericeous-strigose; plants largely eglandular (except for sparse sessile glands on phyllaries), usually with leaves only ca. 2–3 cm long at mid-stem, developing many long stiff branches with abrupt further reduction in leaf size ..... **Symphyotrichum patens var. patentissimum**

5. Involucres campanulate or narrowly turbinate, mostly 5–7.5 mm long; phyllaries in 4–5(–6) series, often somewhat squarrose, acute to acuminate, middle ones 0.7–1.2 mm wide (linear-lanceolate), densely strigillose to almost glabrous; plants glandular (mostly stipitate-) or largely eglandular, with varied leaf size and branching.

6. Mid-stem leaves mostly 3–5 cm long, separated by internodes of (0.5–)1–2(–3) cm at their densest, often adnate-ascending; plants usually 0.4–0.8 m tall [to 1 m in cultivation]; heads mostly 7–11 mm wide.

7. Stems and leaves with dense to sparse stipitate-glands, with or without eglandular hairs; plants somewhat bluish-waxy, often becoming blackish when dried; leaves abruptly reduced in size with each braching order; mid-stem leaves [directly below inflorescence] with length/width (1.5–)2–2.5(–3), clustered and overlapping along 10–20 cm; bracts on proximal thirds of peduncles mostly 1–2(–3) mm wide ..... **Symphyotrichum patens var. terranigrum**

7. Stems and leaves generally eglandular (except sometimes for scattered glands on distal branches), but with dense ascending eglandular hairs; plants usually dull greyish-green, not much darkening when dried; leaves usually with gradual or irregular reduction from base of stem to summit; mid-stem leaves with length/width (2–)2.5–4(–4.5), not forming a distinct overlapping cluster; bracts on proximal thirds of peduncles mostly 2–3(–5) mm wide ..... **Symphyotrichum patens var. gracile** [This taxon may not be clearly separable from the "widespread typical variant" keyed out below under 8.]

6. Mid-stem leaves mostly 5–7 cm long, separated by internodes of (1–)1.5–3(–4) cm at their densest, usually spreading; plants usually 0.8–1.6 m tall; heads mostly 9–12 mm wide.

8. Leaves and stems with stipitate glands densely or sparsely scattered among longer glandular hairs; leaves usually somewhat bluish-green when dried; inflorescences usually less branched, ca. 10–30 cm wide, with peduncles mostly (1–)2–7(–9) cm long ..... **Symphyotrichum patens**, largely Appalachian variant [Some of these plants appear transitional to *S. phlogifolium*; see also "large-leaved plants from Mississippi and Tennessee" in notes below.]

8. Leaves and stems without glands, usually dull greyish-green when dried; inflorescences usually much branched, ca. 30–50 cm wide, with peduncles mostly (4–)6–10(–13) cm long ..... **Symphyotrichum patens**, widespread typical variant

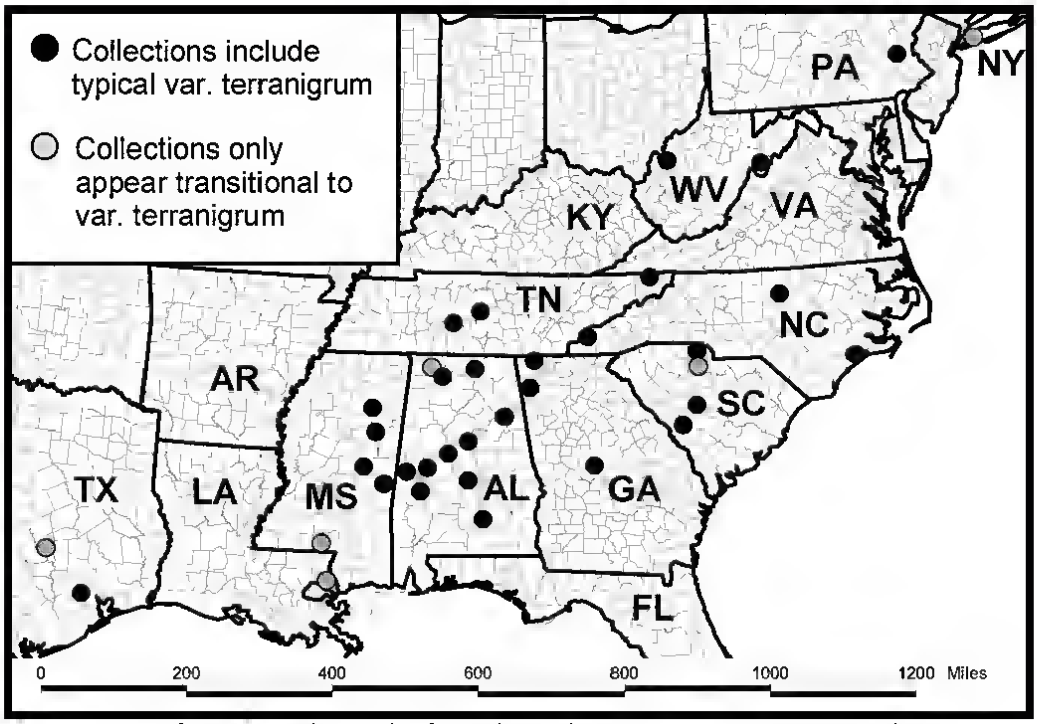

Figure 4. Map of counties with records of *Symphyotrichum patens* var. *terranigrum* and apparent transitions to var. *gracile* or var. *patens*. See text for sources of data.

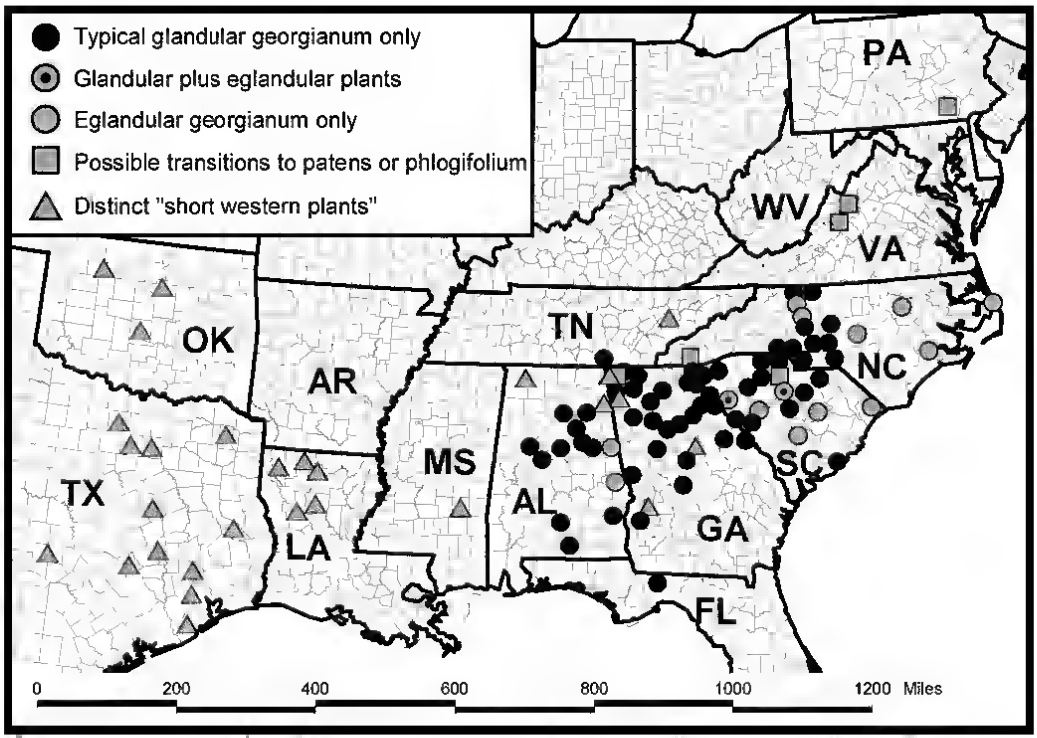

Figure 5. Map of counties with records of *Symphyotrichum georgianum* or *georgianum*-like plants. See text for explanation of taxa and sources of data.

Notes on taxa

These are provided in a provisional taxonomic order. Asterisks below indicate associated species that are more common on base-rich soils; double asterisks indicate stronger concentration.

Symphyotrichum patens. It has been difficult to maintain consistent segregates within this species and definitive molecular studies are still needed, but the following five or six entities can be tentatively outlined. *Symphyotrichum patens* is highly variable in glandularity, sizes and shapes of leaves, branching patterns of inflorescences, and head sizes. Further clarification is needed regarding rhizomes. Brouillet et al. (2006) noted this: "cespitose; with short, thick, woody caudices, tangled or sometimes cormoid, and long rhizomes." Jones (1983) noted this: "Plants cespitose, with new stems arising in clusters at or near the old stem bases. Underground stem a caudex, or occasionally with short rhizomes." Based on our cultivation of several plants and examination of many herbarium specimens, distinct rhizomes are not formed, except perhaps rarely in a few plants referable to var. *gracile* or to the 'Appalachian variant' noted below. The only described taxon within the whole *S. patens* group that regularly has distinct rhizomes appears to be *S. georgianum*. Further clarification is also needed in chromosome numbers. It is suggested here that var. *terranigrum* and var. *gracile* largely correspond to the mapped concentrations of diploids within *S. patens* on the Coastal Plain (Nesom 2006), but there are probably exceptions (R. Jones 1980). For example, a plant collected from West Virginia assigned above to var. *terranigrum* was determined to be tetraploid: *Semple & Chmelewski 5893* (MO), under the name "*Aster phlogifolius*." Also, a hexaploid has been recorded under var. *patens*; see below.

S. patens* var. *terranigrum. See notes under description above.

S. patens* var. *gracile (Hook.) Nesom [= *Aster tenuicaulis* (C. Mohr) Burgess]. These plants are relatively slender, with long, minutely bracteate flowering branches and relatively small heads with little glandularity. In a few collections at BRIT from Texas (Comanche, Dallas, and Denton cos.), rhizomes are present, suggesting transitions to the "short western plants" outlined below. Jones (1983) mapped var. *gracile* no further east than Alabama. Brouillet et al. (2006) stated that it "is most common in the southwestern part of the species range... It is mostly diploid, some tetraploids occurring in Texas and Louisiana." But, following Cronquist (1980), they also recorded it as far east as Maryland. Nesom (2006) could not discern any discontinuity from typical var. *patens*, noting typical var. *gracile*-like plants through "part of the range of var. *patens* ... commonly northeastward at least into North Carolina." From general review of collections for this paper, plants referred to var. *gracile* using the key above are concentrated on the Gulf Coastal Plain, from Oklahoma and Texas to Georgia and Florida. Further work is needed to refine the morphological and cytological basis for distinction and to provide a more precise map.

Because ecologists have generally not recognized var. *gracile*, details of its habitat are not well documented. Nevertheless, it is likely that much of the "*Symphyotrichum patens*" recorded in *Pinus palustris* woodland can be referred to this variety (Mohr 1903; Penfound & Watkins 1937; Peet & Allard 1993; Kush et al. 2000; Maceina et al. 2000). Peet and Allard described three types of longleaf pine woodland with *S. patens*: Piedmont Upland, Southern Subxeric, and Southern Mesic. The most common trees and shrubs in these types are *Pinus palustris* (usually dominant), *Diospyros virginiana*, *Quercus marilandica*, *Q. margarettiae*, *Q. incana*, and *Vaccinium arboreum*; others include *Aronia arbutifolia*, *Gaylussacia dumosa*, *Hypericum hypericoides*, *Ilex glabra*, *I. vomitoria*, *Oxydendron arboreum*, *P. echinata*, *P. virginiana*, *Q. falcata*, *Q. laevis*, *Q. montana*, *Q. pumila* [= *Q. elliottii*], *V. crassifolium*, *V. elliottii*, *V. fuscatum*, and *V. tenellum*.

***S. patens*, Appalachian variant**. As outlined in the key above, these are plants with scattered glands on leaves and stems, relatively narrow, less branched inflorescences, and disc corollas that often turn

purple at tips. These characters suggest a transition from *S. patens* var. *patens* to *S. phlogifolium*, which shares the same typical chromosome number (2n = 20); and Jones (1983) was able to make hybrids in cultivation. But in a few collections there appear to be distinct rhizomes, suggesting transitions to *S. georgianum* instead: for example, in old collections from Mass. (*Blake*, 12 Sep 1884, Andover) and Pa. (*Ricksecker*, 28 Sep 1897, Delaware Water Gap) at MU. This 'Appalachian variant' was recorded from the following states: Ala., Conn., Ga., Ind., Ky., Mass., N.Car., N.H., N.J., N.Y., Ohio, Pa., S.Car., Tenn., Va., W.Va. Its range is about the same as that of *S. phlogifolium*.

***S. patens*, large-leaved plants from Mississippi and Tennessee** (not separated in key above). There are a few unusual collections of *S. patens* with little glandularity, exceptionally large primary leaves (mostly 15–25 mm wide) and relatively short peduncles (mostly 1–10 cm). These plants do not fit readily into any of the described *patens* varieties. They occur mostly in more mesic situations: examples include *Simmons CL-689* (MMNS) from Clay Co., Miss.; *Morgan 1473* (MMNS, IBE) from Jones Co., Miss.; *Sullivan 05-111* (MMNS) from Lee Co., Miss.; *Meeks 363* (IBE) from Tippah Co., Miss.; *Brooks 555* (IBE) from Webster Co., Miss.; *McNeilus 89-991* (TENN) from Cumberland Co., Tenn.; and *Clements 570* (TENN) from Franklin Co., Tenn. Some of these plants have been confused with *S. phlogifolium*.

S. patens* var. *patens. This common variant of *S. patens* lacks glands on leaves and stems, and generally has robust, widely spreading inflorescences. Almost all chromosome counts have indicated tetraploid status, with 2n = 20 (Nesom 2006). However, Semple recorded 2n = 30 on the label for his collection *10984* from Walker Co., Georgia (BRIT, WAT). In Figure 5, this collection is included with "possible transitions" to *S. georgianum*, which is the only taxon in the *patens*-complex that has 2n known to be more than 20.

Var. *patens* is widespread across southeastern states, but uncommon to absent in some warmer sections of the Coastal Plain, in some cooler sections of the central Appalachian Mountains, and in the Ozark-Ouachita region. It is most common in thin dry woods and grassy openings on strongly to moderately acid soils. Typical woody plants in optimal habitat include *Pinus echinata, Quercus marilandica*, and *Q. stellata* (locally dominant) plus *Carya ovata, C. glabra, C. tomentosa, Cornus florida, Nyssa sylvatica, P. virginiana, Q. alba, Q. coccinea, Q. falcata, Q. montana, Q. velutinum, Rhus copallina, Sassafras albidum, Vaccinium arboreum, V. pallidum*, and *V. stamineum* (NatureServe 2014: associations CEGL 4756, 5018, and 7500).

S. patens* var. *patentissimum. This largely replaces typical var. *patens* in most of Arkansas and Missouri, plus minor parts of Oklahoma, Kansas, and Illinois, but intermediate plants do occur in zones of overlap (Nesom 2006). There are also records from Texas, Louisiana, Mississippi, and Kentucky, as reviewed by Nesom, but these have mostly been somewhat dubious or the plants appear intermediate. For Kentucky, there is a collection from Graves Co. that is referable to var. *patentissimum* (*Athey 466* at EKY). But other reported collections appear no more than intermediate: from Hickman Co. (*Grubbs 1214* at GA & MUR); and from McCracken Co. (*Athey 2143* at BRIT, MO, and NCU).

Within the Ozark and Ouachita Mountains at the center of its range, optimal habitat appears to be thin woods with rocky glades (often on somewhat base-rich sandstones and shales), or dry grasslands with moderately acid soils. Typical woody associates include *Quercus stellata* (locally dominant) plus *Carya texana, Celtis tenuifolia***, *Fraxinus americana** [sensu lato], *Juniperus virginiana**, *Pinus echinata, Prunus americana** [sensu lato], *Rhus copallina, Ulmus alata**, and *Vaccinium arboreum* (NatureServe 2014: associations CEGL 7814 and 7824).

Symphyotrichum phlogifolium. This species is largely Appalachian, but details of its western range need to be clarified (Figure 1). In Kentucky, there are a few scattered records from the western Knobs and Shawnee Hills, to be verified in some cases (Jones 1983, 1992; J. Campbell and M. Medley, in prep.). It has also been reported from southern Indiana (Jones 1983) and perhaps southern Illinois (USDA 2014a). However, in Tennessee *S. phlogifolium* remains unknown west of Appalachian regions (Chester et al. 1997; D. Estes, pers. comm.), and the record from Mississippi (Cronquist 1980) remains dubious. Jones (1983) showed that this species can cross readily with *S. patens* in cultivation. Hybrids have not yet been proven to exist in the wild, but suggestive collections include the following: *Kral 70974* from Marshall Co., Alabama (VDB); *Cronquist 4798* from Walker Co., Georgia (BRIT); and *Hammer 173* from Gallia Co., Ohio (VDB). Also, collections noted above under the "Appalachian variant" of *S. patens* may be interpreted in terms of introgression from *S. phlogifolium*. And at least one collection from North Carolina suggests a transition to *S. georgianum* (see below).

Typical habitats for *Symphyotrichum phlogifolium* are thin woods and edges in partial shade on subxeric to submesic slopes with moderate to low soil acidity. Based on personal experience, on collection data (especially at BRIT-VDB), and on published surveys (e.g., Hardin 1988, Kauffman et al. 2004, Marx 2007, Thompson 2008, Larson 2011), *Quercus alba* is among the most commonly associated trees; other species include *Acer rubrum, A. saccharum*, Carya glabra, C. ovata*, Diospyros virginiana, Fraxinus americana** (sensu lato), *F. quadrangulata**, Juniperus virginiana*, Liriodendron tulipifera, Pinus strobus, Platanus occidentalis, Prunus serotina*, Q. coccinea, Q. muhlenbergii**, Q. rubra, Q. shumardii**, Q. velutina, Sassafras albidum, Tsuga canadensis*, and *Ulmus rubra**. At some localities, rocky glades or grasslands are intermixed with wooded habitats. The species is rare to absent within more mountainous sections of the Appalachians and where strongly acid soils predominate.

Symphyotrichum georgianum. The range of this species is centered on the Piedmont of Alabama (in a small disjunct section), Georgia, South Carolina, North Carolina, and possibly (with atypical plants) Virginia to Pennsylvania (Figure 5). It also extends north into the adjacent Ridge-and-Valley and onto the southern Cumberland Plateau, especially in Alabama, and there are a few records from the central Coastal Plain south to Leon Co., Florida (Weakley 2012). Collections from the counties listed below were verified at the herbaria shown in parentheses. *S. georgianum* is reported here from Tennessee for the first time, based on a collection that had been filed under *S. patens*. In addition, there are a few old collections from Pennsylvania and Virginia that appear intermediate between *georgianum* and *patens*; see also notes above under the 'Appalachian variant' of *patens*. Several other misidentifications or questionable identifications were discovered, and records of atypical 'eglandular plants' are provided in the subsequent section.

On the Piedmont, typical habitat is dry thin woodland and grassland on basic hardpan soils (formed from diabase, dolomite, kyanite, etc.), probably maintained by frequent fire before settlement (Weakley 2012). Typical woody associates, based on the literature plus collection data, include *Quercus stellata* and *Q. marilandica* (both locally dominant before settlement) plus *Cercis canadensis*, Cornus florida, Hypericum prolificum*, Ilex longipes, Juniperus virginiana*, Pinus echinata, P. palustris, P. taeda, Quercus velutina, Symphoricarpos orbiculatus*, Vaccinium arboreum*, and *Viburnum rafinesquianum** (Tompkins 2013; NatureServe 2014: association CEGL 3711). However, mostly different associates were reported on Cambrian (Ketona) dolomite of the disjunct Piedmont in Bibb Co., Alabama (Allison & Stephens 2001), and on Eocene chalk of the Coastal Plain in Houston Co., Georgia (Echols & Zomlefer 2010). At both localities, *S. georgianum* is rare but it occurs in grassland and brushy transitions similar to the Black Belt habitat of *S. patens* var. *terranigrum*; associates include a much higher proportion of calciphiles than for *S. georgianum* further east.

***Symphyotrichum georgianum*, typical glandular plants**. Following are recorded counties, with abbreviated data. Question marks (? before states or acronyms) indicate uncertain identifications, usually due to incomplete collections.

Alabama: Bibb (EKY), Barbour (VDB), Blount (BRIT, GA, VDB; *Kral 37826,* "rays deep violet, very lovely and perhaps the finest aster I have ever seen"), Butler (VDB), Calhoun (VDB), Clay (VDB), Covington (NCU), Etowah (GA, VDB), Shelby (VDB), St. Clair (EKY, VDB). Jones (1992), Allison & Stevens (2001) and USDA (2014a) add, for the species, Talladega and Tuscaloosa cos. **Georgia**: Clarke (GA), Chatooga (GA), Dawson (BRIT, GA, NCU), Elbert (GA), Fulton (GA), Habersham (US), Harris (GA), Houston (GA), Jones (BRIT), Madison (EKY, GA, VDB), McDuffie (BRIT), Rabun (GA), Randolph (GA, US), Richmond (EKY), Rockdale (BRIT, GA, US). Jones (1983) adds, for the species, Catoosa, Cherokee, Hart, Walton, and Warren. USDA (2014a) adds Spalding for the species, while M. Medley and R. Ware (pers. comm.) have recorded it from Gordon, Murray, and Paulding. An additional old collection that is probably from Fulton Co. may be transitional to the "short-western plants" outlined below: Atlanta, damp shady copses, 22 Oct 1888, "*Aster patens* var. *georgianus*" of *Mohr s.n.* (?US). **North Carolina**: Gaston (EKY, NCU, US), Mecklenberg (EKY), Montgomery (NCU, VDB), Randolph (NCU), Richmond (NCU), Rowan (EKY), Stanly (NCU, VDB), Stokes (NCU), Surry (NCU), and Union (EKY, VDB). There is also an odd collection grown from Macon Co. that was initially identified as *S. phlogifolium*, but it suggests more similarity to *S. georgianum* (*Semple 10856* at NCU). ?**Pennsylvania**. Lancaster Co.: "about the mouth of the Tucquan in Eozoic" [sic], 20 Sep 1901, *Heller s.n.* (?US). This incomplete collection appears to have a rhizome; it suggests *S. georgianum* or a transition to *S. patens*. **South Carolina**: Abbeville (GA, USCH), Charleston (NCU), Cherokee (EKY, NCU, USCH, VDB), Chesterfield (GA), Edgefield (GA, NCU, USCH), Fairfield (EKY, USCH), Kershaw (NCU), Laurens (EKY), McCormick (BRIT, GA, NCU, US), Oconee (BRIT, GA), Pickens (US), Richland (GA, EKY, USCH), York (EKY, NCU, USCH). Jones (1983, 1992) adds Union for the species. There is also an odd collection from Chester Co. that suggests a transition to *S. patens* (*Horn 6241* at US). **Tennessee**. Marion Co.: steep limestone slope by US 41 ca. 4 mi SSE of Monteagle, 7 Oct 1969, *Kral 37623* (GA). ?**Virginia**. Augusta Co.: vicinity of Fordwick and Craigsville in Allegheny Mts., alt. 480 m, 14 Sep 1913, *Steele 190* (?US). Rockbridge Co.: vicinity of Goshen in the Alleghenies, 425 m alt., 11 Sep 1904, *Steele s.n.* (?US). Both of these collections lack sufficient plant base to show rhizomes, but they have *georgianum*-like leaf texture, dense glands on leaves and stems, and relatively large heads on long ascending branches. It is possible they are intermediate in some way between *S. georgianum* and *S. patens*.

***Symphyotrichum georgianum*, largely eglandular plants**. At least some of the collections from the following counties have few or no glands, except at phyllary tips. Otherwise they are similar to typical *S. georgianum*. These plants have been recorded for certain only from the Carolinas, but it is likely that eglandular plants will be confirmed in Georgia and Alabama. Several of the older records of "typical glandular *georgianum*" (see above) may not have been double-checked for the presence of glands. Eglandular plants are concentrated further east than typical *S. georgianum*, extending onto the Atlantic Coastal Plain (Figure 5). Their range is similar to that of *S. grandiflorum*, which Jones (1983) suggested might be involved in the ancestry of *S. georgianum*. ?**Alabama**: Randolph (?VDB; lower parts missing), Lee (?VDB; rhizome not clear). **North Carolina**: Dare (NCU), Davie (NCU), Jones (NCU), Lee (NCU), Nash (NCU), Yadkin (NCU). **South Carolina**: Abbeville (NCU), Fairfield (NCU), Horry (USCH), Orangeburg (NCU), Saluda (NCU), Sumter (USCH).

Symphyotrichum* sp., aff. *georgianum, here informally named "short western plants." In searching through folders of *S. patens*, the following distinct but variable collections were discovered from scattered sites on the Gulf Coastal Plain and southern Cumberland Plateau, mostly on sandy soils; a selection is shown in Figures 6a-f. Most of them resemble *S. georgianum* in having relatively large heads, more or less corymbiform inflorescences with ascending branches, distal leaves not strongly auriculate-amplexicaul, and in some cases they are clearly rhizomatous. Unlike typical *georgianum*,

these plants are relatively short; several do not appear to have distinct rhizomes; and glands are often sparse to absent. The key above summarizes observations for this whole group of collections. Collections that have rhizomes are indicated below by "/ R" after herbarium acronyms; collections that are glandular below the inflorescence are indicated by "/ G" (lower case indicates character not clearly expressed).

Alabama. Cherokee Co.: ca. 2 mi W of Jamestown, SW4 S29, Lookout Mountain, cut-off and burned area, occasional, 11 Oct 1986, *McDaniel 29161* (IBE, VDB / G). Colbert Co.: just S of Muscle Shoals and river by Ala. 17, sandy silt of oak flats, 21 Oct 1976, *Kral 59430* (VDB / G). **Georgia**. Dade Co.: roadbank of I-59 0.1 mi from Alabama line south of Rising Fawn, 15 Oct 1989, *R.D. & B.G. Thomas 113,837* (TENN / Gr). Floyd Co.: common, cliffs of the Coosa, above Blacksbluff Road near Rome, S of quarry on Colbert very rocky silt loam over clay and Conasauga limestone, 20 Oct 1968, *Lipps et al. 4037* (BRIT, limited basal collection, but heads very compact on branches only ca. 1 cm long). ?Putnam Co.: SW of Warfield US-129 SW of Little River, near Old Macon Crescent (MP-5), 6.3 km N of GA-212, disturbed area, full sun, red clay, 18 Oct 1999, *Semple 10874* (WAT, GA, BRIT, "2n = 20"; very few/no glands, and also mounted on sheet is piece with much smaller leaves). **Louisiana**. Bossier Par.: sandy soil near Haughton, 12 May 1925, *Palmer 27166* (MO / R? but depauperate collection). Claiborne Par.: drier portions, open sandy slough and seepage area, 18 mi SW of Junction City, 29 Oct 1964, *Kral 23238* (VDB). Lincoln Par.: Woodland Park off La Hwy 146, Ruston, open upland mixed forest, clay seepage area, N 92° 37' W 32° 32', 4 Nov 1988, *Purifoy 75* (MU). Natchitoches Par.: 3 mi E Robeline, burned over sandy loblolly pine stand, 27 Oct 1962, *Kral 16138* (VDB). Webster Par.: [no location], 7 Nov 1971, *Thompson 6* [Southeastern State College] (BRIT, only 15 cm tall). Winn Par.: recently cleared and burned longleaf pine woods besides USFS Rd 554, 0.5 mi N of La 126 and La. 1233 in Kisatchie National Forest N of Pine Ridge, Sec. 8 T13N R5W, 16 Nov 1990, *Thomas 122829* (GA, MU / gr). [Note that R. Jones (1980) initially mapped *S. georgianum* in Louisiana, but based on a "dubious, mixed collection" (Jones 1983) that needs to be compared with these plants.] **Mississippi**. Jasper Co.: Tallahala Wildlife Management Area; ca. 0.3 mi W of Randall Hill Cemetary; T4N R10E Sec. 13 NE4 NW4, common throughout area, 25 Oct 1988, *Carraway 467* (IBE / g). **Oklahoma**. Cleveland Co.: dry hillsides 8 mi E of Norman, 10 Oct 1924, *Bruner s.n.* (BRIT / r). Major Co.: sandy soil 14 mi NE of Seiling, 25 Aug 1927, *Stratton 471* (MO). Payne Co.: clay loam soil 5 mi E of Stillwater, 29 Sep 1932, *House 71* (MO). These collections have relatively small heads, short leaves, no glands on stems or leaves, tight clumps only ca. 30–35 cm tall. **Tennessee**. Knox Co.: Cherokee Bluffs, Knoxville, limestone under rich loamy soil, woods edge, 3 Oct 1965, *Morton 420* (BRIT / G). Roan Co.: wasteground, Mt. Roosevelt State Forest, ca. 2 mi W of Rockwood along Hwy 70, 21 Oct 1984, *McKinney 3415* (VDB; G). **Texas**. Angelina Co.: rolling sandy longleaf line area above lake at Boykin Springs, Angelina National Forest, 30 Nov 1962, *Correll 26863* (BRIT). Brazoria Co.: Nash Ranch, 275 acre hay meadow W of CR 25 ca. 8.7 mi N of intersection with Hwy 35 in West Columbia, infrequent in drier places with *Panicum* spp., *Muhlenbergia capillaris, Schizachyrnum scoparium, Rhynchospora* sp., and *Paspalum plicatum*, 27 Oct 2005, *Rosen 3597* (BRIT; R). Brazos Co.: Minter Springs 11 mi SW of Millican, stems 6 dm high or more along a creek, 8 Nov 1945, *Cory 50591* (BRIT, US / R; leaves with thick margin like *georgianum* but relatively open diffuse inflorescence that suggests *S. patens* var. *gracile*); low moist area on sandy soil in partial shade, along White Creek, A&M College Swine Unit W of main campus, 16 Nov 1951, *Conrad 385* (BRIT / r). Dallas Co.: "sandy woods" or "Dallas sands", 1880, *Reverchon 4360* (MO, US; "*Aster patens* var. *gracile*" or "*Aster subsessilis* Burgess"; no glands even on phyllaries, rather dense corymbiform inflorescence). Gillespie Co. [?]: "Geb [?] Hollow, Gillespie"; "*from the coll of G. Jermy" s.n.* (MO, purchased 1897 / r). Harris Co.: prairies, Houston, Sep 1842, *Engelmann s.n.* (MO / gR); sandy loam, much leaves among grass, clearing in woods under *Pinus, Quercus, Vaccinium*, and grasses, ca. 0.2 mi N of Buffalo Bayou and 250-300 yards E of Post Oak Rd., Houston Memorial Park, 25 Oct 1956, *Traverse 247* (BRIT / R). Lee Co.: roadside adjacent to oak forest, deep sandy soil, 1.7 mi on 77 N of jct. 21 and 77, 28 Oct 1983, *Mahler 9698* (BRIT / R). Limestone Co.: post oak savannas, Hwy 14 and park road 28, Fort Parker

State Park, Aug 1993, *Singhurst et al. 1308* (BRIT / R). Montgomery Co.: 2.25 mi S of Willie, freq. in sandy pineland, 10 Nov 1945, *Cory 50678* (BRIT / R). Tarrant Co.: sandy soil, Lake Worth, 10 Sep 1924, *Ruth 421* (BRIT; R); post oak belt, Eagle Mountain Lake, E side near boat club, 12 Oct 1946, *Whitehouse 17334* (BRIT / R). Titus Co.: blooming after mowing, 3 mi W Mt. Pleasant on Hwy 67 near bridge over small creek, 2 Nov 1946, *Whitehouse 17750* (BRIT). Wise Co.: CR 2445, sandy roadside at 253 m elevation, N33° 20' 13.48", W97° 32' 54.28", 26 Sep 2003, *O'Kennon & McLemore 19049* (BRIT / R)

Further discussion of ecology and range of var. *terranigrum*

The Appendix (web address after Literature Cited) organizes information above on typical habitats of taxa within the *Symphyotrichum patens* complex in terms of compositional gradients among woody associates. It indicates that the taxa are largely segregated along such gradients except for *S. patens* var. *patentissimum* and *S. georgianum*, which have ranges that do not overlap at all.

Across most of its range, *Symphyotrichum patens* is typical of medium to strongly acid soils. Var. *patens* is infrequent on calcareous soils, but often occurs around calcareous glades where more acid material has slumped or washed in from above. Var. *gracile* is typical of acid sandy soils on the Coastal Plain; see also Mohr (1901). Var. *patentissimum* is typical of moderately acid soils in the Ozark-Ouachita region; see also Yatskievytch (1999). These observations are supported by descriptions of varied grassland and woodland types, as summarized by NatureServe (2011) and detailed in numerous regional or local studies. For example, Campbell et al. (1989, 1991) listed typical *S. patens* as a frequent species in remnants of 'sandy barrens' (open grassy woodland) on acid soils of the Cumberland Plateau, but Lawless et al. (2006a, b) did not report it at all from the 'xeric limestone prairies' of Kentucky or elsewhere in east-central states. In contrast, var. *terranigrum* appears largely restricted to xeric calcareous soils, mostly on or near the Coastal Plain of southeastern states (Figure 4). Its fragmented known range reflects the limited occurrence of such habitats in this region. To the north of its clustered records in the Black Belt of Alabama and Mississippi, it is largely unknown on limestones of the Interior Low Plateaus, but its ecological place there is taken by other asters, including *S. oblongifolium* (Nutt.) Nesom and *S. pratense* (Raf.) Nesom, both in subg. *Virgulus*.

Disjunct records of plants resembling *Symphyotrichum patens* var. *terranigrum* to the northeast of the Black Belt, as far as LeHigh County, Pennsylvania, and Nassau County (Long Island), New York, are provocative (Figure 4). Pretz's 1917 collection from Pennsylvania does not appear to have been part of a published flora, although he did start a series (Pretz 1911). Laughlin and Uhl (2003) reported that there are still remnants of 'xeric limestone prairies' in this Ridge-and-Valley section of the state, although none are currently known in the Great Valley of LeHigh County. Ten of the 12 state-listed rare species that Laughlin and Uhl noted as associated with such prairies in Pennsylvania also occur in the Black Belt, often growing with *S. patens* var. *terranigrum* or nearby in Mississippi: *Boutelova curtipendula*, *Dichanthelium oligosanthes*, *Limum sulcatum*, *Lithospermum canescens*, *Onosmodnum hispidissimum*, *Ophioglossum engelmannii*, *Ranunculus fascicularis*, *Ruellia humilis*, *Senna marilandica*, and *Solidago rigida*. Despite the virtual eradication of their original

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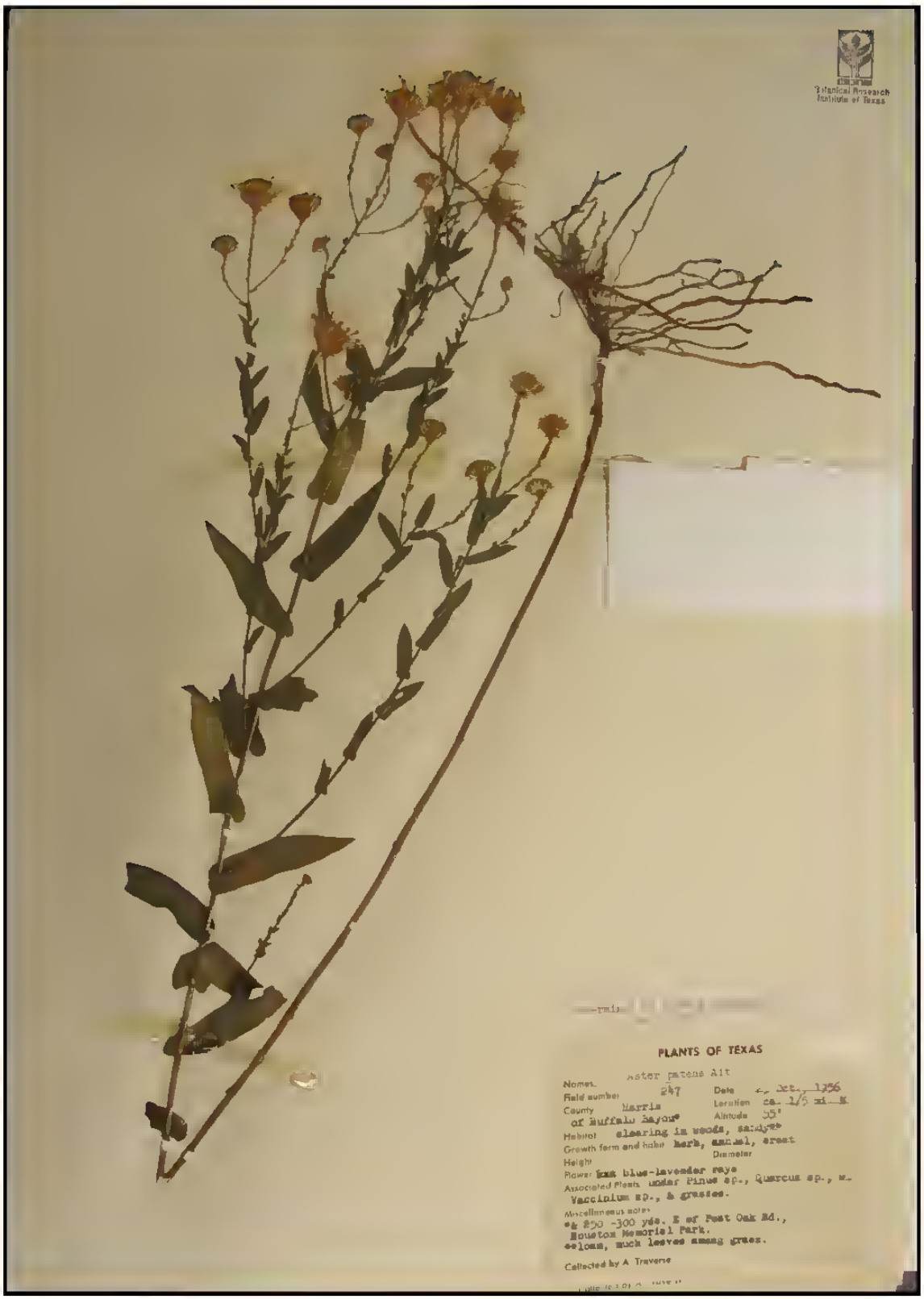
Figures 6a to 6f [on next six pages]. Examples of *Symphyotrichum* aff. *georgianum*, undescribed "short western plants"; see details of collection data in text above.
(a) *Carraway 467* from Mississippi (IBE)
(b) *Kral 23238* from Louisiana (VDB)
(c) *Engelmann s.n.* from Texas (MO)
(d) *Reverchon 4360* from Texas (MO)
(e) *Traverse 247* from Texas (BRIT)
(f) *House 71* from Oklahoma (MO).

COMPOSITAE
Aster patens Ait. var. patentissimus (Lindl) T. & G.
MISSISSIPPI. Jasper Co.: Tallahala Wildlife Mngmt area, ca 0.3 miles W of Randall Hill Cemetary. T4N R10
S13 NE4 NW4, rays blue, disks yello
Common throughout area.
October 25, 1988
Daniel T. Cairaway 46
Institute for Botanical Exploration (IBE)

HERBARIUM
VANDERBILT UNIVERSITY
VDB
15316
PLANTS OF LOUISIANA
Claiborne Par. 29 Oct 1964 A.Kral 21238
Aster patens
Drier portions. Open, sandy slough and seepage area 18 mi. s.w. Junction City.
det A.Kral
Aster patens Ait. var. gracilis Hook.
Examined in a revision of Aster section Patentes (Asteraceae).
Ronald L. Jones 1970 Vanderbilt University

TEXAS
Collected by F. Lindheimer.
George Engelmann, M D
St. Louis, Mo.

5001


Botanical Research Institute of Texas
PLANTS OF TEXAS
Name. Aster patens Ait
Field number 247
Date Oct., 1956
County Harris
Location ca. 1/5 mi. N.
of Buffalo Bayou
Altitude 35'
Habitat clearing in woods, sandy
Growth form and habit herb, annual, erect
Height
Diameter
Flower lax blue-lavender rays
Associated Plants cedar Pines sp., Quercus sp., V.
Vaccinium sp., & grasses.
Miscellaneous notes
ca 250 -300 yds. E of Post Oak Rd.,
Houston Memorial Park.
soloam, muck leaves among grass.
Collected by A Traverse

vegetation, these species remain clustered in southeastern counties of Pennsylvania. It is likely that further inventory of old roadsides, rough unimproved pastures, and other grassland remnants on calcareous soils throughout the Ridge-and-Valley will provide additional records of var. *terranigrum*.

The 1893 collection by Joseph Schrenk from Hempstead Plains on Long Island, New York, is more difficult to interpret. It does match *Symphyotrichum patens* var. *terranigrum* in its dense glands and dark crowded leaves, but the habitat is not typical. Original soils of these plains appear to have been formed mostly in a silty mantle on strongly acid sand and gravel outwash deposits. Further investigation of soils in this region could be useful; the original A horizon of the Hempstead soil series was a "black silt loam" with moderate acidity that has probably been reduced by erosion after settlement (USDA 2014b). The previously documented flora does not include any *S. patens*, and there are virtually no calciphiles listed (Stalter & Seyfert 1989). Faunistic evidence supports the concept of a periglacial origin for this ecosystem, with little connection to southeastern grasslands (Hamilton 2012).

A fundamental question arises. Do real biogeographic connections exist among these cited collections of *Symphyotrichum patens* var. *terranigrum*, through dispersal from a common ancestor? Or do some of these plants have independent origins from a broader gene-pool of the whole species? In addition to more molecular analysis, deeper understanding of relationships with herbivores could eventually help with this question. It is likely that glands in these plants, like other Asteraceae, have some function in deterring herbivores and that their frequency in populations is influenced by genotypic selection as well as by environmental effects on plant development (e.g., Levin 1973; Kelsey et al. 1984; Guillet et al. 1997). Moreover, larger herbivores could have promoted long-distance dispersal of seed in fur or gut (e.g., Myers et al. 1997; Rosas et al. 2008). Dispersal by bison and other large animals, now extinct, may well have been concentrated along calcareous "barrens" and fertile lowlands of the Ridge-and-Valley region (DeSelm 1994; Brown 2000; McDonald 2000; DeSantis & Wallace 2008) and along base-rich "prairies" of the Atlantic Piedmont (Schmidt & Barnwell 2002; Tompkins et al. 2010).

Discussion of the *Symphyotrichum patens* complex in general

Taxonomy of the *Symphyotrichum patens* group remains unsettled for several reasons. As in several other large genera of Asteraceae, the gross morphology of individual species is often plastic, defying description of consistent differences in branching pattern, leaf-shape, or pubescence. Even with flowering heads, careful observation and precise descriptive language is sometimes inadequate to distinguish taxa based on single characters. Moreover, it seems likely that the divergence of taxa has been relatively recent and reticulate — resulting in occasional intermediate forms, hybrids, or otherwise atypical plants, especially among polyploids.

The primary division here — couplet 1 of the key above — remains tentative in its language. For previous treatments, *Symphyotrichum georgianum* has been distinguished using several characters: rhizomatous habit, leaves thick-textured, with revolute margins, and less clasping, at least distally, and larger heads, mostly notably in the rays (Jones 1983; Brouillet et al. 2006). After examination of much typical *georgianum*, plus other affiliated plants, it is reasonable to add emphasis of the relatively compact inflorescences with ascending branches, which are usually evident in collections. However, given the suggested alliance with anomalous "short western plants," one has to loosen up the ray size and rhizome characters in couplet 1. When those plants are better understood, the key can probably become more definitive. Without direct experience of them in the field, it was considered premature here to make a final judgement as to taxonomic status.

A more thorough survey of chromosome numbers is still needed within the whole *Symphyotrichum patens* complex, together with further taxonomic assessment of collections

vouchering previous counts. As noted above, it is likely that var. *terranigrum* and var. *gracile* partly correspond to the two clusters of diploids (2n = 10) previously mapped east and west of the Mississippi River, respectively. These two groups of plants tend to be associated with seasonally xeric open habitats on calcareous (var. *terranigrum*) or non-calcareous (var. *gracile*) soils, mostly on or near the Coastal Plain. Tetraploids (2n = 20) have become more widespread across southeastern states (typical var. *patens*), or concentrated around the Ozarks (var. *patentissimum*) and Appalachians (*S. phlogifolium*). They tend to occur in more densely wooded landscapes, especially the relatively large-leaved *phlogifolium*.

Typical plants of the decaploid (2n = 50) *Symphyotrichum georgianum* deserve deeper analysis in relation to the variants suggested above and in relation to Jones' (1983) hypothesis that this species originated from hybridization of *S. patens* var. *patens* (2n = 20) and *S. grandiflorum* (2n = 30, 60). The robust growth form of *S. georgianum* is presumably well-suited to the oak savannas and glades that are its native habitats. Rhizomes in grassland may have some general value related to moderate disturbance from browsing or burning on locally more fertile soils, following the rationale of Craine et al. (2001), N'Guessan (2007), and others. Unfortunately, this species has become generally imperiled within its small range (NatureServe 2014), and its original ecology remains somewhat obscure.

The phylogenetic and functional significance of stipitate glands deserves further attention. This character is central to distinction of *Symphyotrichum patens* var. *terranigrum* and of several other taxa within subg. *Virgulus* at various taxonomic levels. Morphological patterns suggest that it is an ancestral character within sect. *Grandiflori* (sensu lato), where it is retained in all taxa, and within sect. *Patentes*, where it is lost in several taxa (Brouillet et al. 2006). Table 1 summarizes the occurrence of glands within these sections and suggests a potential relationship with the base-status of typical soils for each taxon. There is an association between "sparse to dense" or "dense" glands (coded at least "2 or 3") and base-rich soils ("BASIC" or "basic"): $P < 0.01$ with Fisher's exact test. However, a more rigorous analysis is needed.

Distinctly stipitate (= "stalked") glands or glandular hairs are uncommon on stems or leaves below the inflorescence among angiosperms of eastern North America. There are a few additional Asteraceae, mostly with short stalks (in *Artemisia*, *Heterotheca*, *Pseudognaphalium*). Other examples include some *Cannabis sativa* (Cannabaceae), *Cuphea viscosissima* (Lythraceae), both species of *Juglans* (Juglandaceae), several species of Caryophyllaceae (in *Cerastium*, *Holosteum*, *Silene*), Onagraceae (in *Circaea*, *Oenothera*), Solanaceae (in *Nicotiana*, *Physalis*, *Solanum*), and Lamiaceae (in *Scutellaria*, *Trichostema*). General knowledge of these species suggests a broader association between stipitate glands and base-rich soils, with correlated variation among closely related taxa in some cases (e.g., loss from *Trichostema brachiatum* to *T. dichotomum* to *T. setaceum*). As noted above, such patterns may involve deterrence of herbivores by the glands before the foliage itself is eaten. And there is increasing evidence for the global principle that herbivory tends to increase on more fertile soils (e.g., Scholes 1990; Edwards et al. 2000; Eskelinen 2008; Smit et al. 2009).

Table 1 [next page]. Potential relationship of glandularity to typical soil base-status among taxa of *Symphyotrichum* subg. *Virgulus* sect. *Patentes* plus sect. *Grandiflori** (sensu lato, indicated by asterisks in first column). This is a provisional exploration, pending more precise descriptions of typical habitats. The probable clade that comprises sect. *Virgulus* plus sect. *Ericoidi* is excluded because those plants have a complete lack of glands, even within the inflorescence, their typical habitats span a wide range of soil base-status. Taxonomy and data come primarily from Brouillet et al. (2006) plus information presented in this paper.

Glandularity is coded as follows. 1 = glands largely restricted to inflorescence.
2 = glands sparse or rarely dense on some leaves and upper stem.
3 = glands sparse to dense on all leaves and most stem.
4 = glands usually dense on all leaves and most stem.

Typical soil for each taxon is based on limited information in several cases.
ACID: concentrated (>80%) on sandy or boggy soils, especially on southeastern Coastal Plain.
acid: common on soils as above, but also frequent to a lesser degree on clays and silts.
ab: poorly known habitats or mixed or intermediate, based on available information.
basic: common on base-rich soils, but also frequent to a lesser degree on more acid soils.
BASIC: concentrated (>80%) on relatively base-rich clays/silts or calcareous soils.

Range is coded as follows, indicating at least the central concentration for each taxon. AC = Atlantic Coastal Plain; AM = Appalachian Mountains and adjacent regions; GC = Gulf Coastal Plain; GP = Great Plains; NE = New England and adjacent Canada; OZ = Ozark and Ouachita region; PM = Piedmont, RM = Rocky Mts , SE = southeastern USA (more or less widely scattered); abbreviations for states are added in some cases for detail.

SPECIES OR VARIETY	GLANDULARITY	TYPICAL SOIL	RANGE
S. patens* var. *gracile	**1**	**ACID**	**GC (TX-FL)**
S. patens* var. *patentissimum	**1**	**ab**	**OZ**
S.* × *amethystinum*	**1**	**ab**	**GP-NE**
S. patens* var. *patens	**1 or 2**	**acid**	**SE**
***S. georgianum*-eglandular**	**1 or 2**	**acid**	**PM-AC**
S. walteri	**1 or 2**	**acid**	**AC (FL-NC)**
***S.* aff. *georgianum*-short western**	**1, 2 or 3**	**acid**	**GC+ (OK-GA)**
S. fontinale	**2**	**ACID**	**GC (FL)**
S. grandiflorum*	**2**	**ACID**	**AC (SC-VA)**
S. pygmaeum*	**2**	**ab**	**Arctic**
S. fendleri*	**2**	**ab**	**GP (central)**
S. adnatum	**2 or 3**	**ab**	**GC (LA-FL)**
S. campestre*	**2 or 3**	**acid**	**RM-CA**
S. yukonense*	**2 or 3**	**basic**	**Arctic**
S. phlogifolium	**3**	**basic**	**AM**
S. novae-angliae*	**3**	**BASIC**	**NE-wide**
***S. georgianum*-typical**	**3 or 4**	**basic**	**PM**
S. patens* var. *terranigrum	**4**	**BASIC**	**SE (MS-AL+)**
S. oblongifolium*	**4**	**BASIC**	**GP-wide**

Priorities for further research

(1) More chromosome counts. Differences in ploidy may be critical for species concepts.

(2) Establishment of living collections. Differences in vegetative growth need better description, and there can also be experiments with growth on varied types of soil. Also, potential hybridization can be investigated.

(3) More detailed genetic and molecular investigation. The taxonomy presented here will be tested.

(4) General synthesis of data for a thorough revision. In addition to phylogeny, some questions of taxonomy will deserve further consideration. At what rank should *Symphyotrichum patens* and its closest allies — versus S. *georgianum* and its apparent "short western" allies — be recognized? At what rank should *S. patens* var. *patentissimum* be recognized?

(5) Experimental comparisons of glandular versus non-glandular plants when subjected to herbivory in varied ecological contexts.

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APPENDIX

Typical Habitats of *Symphyotrichum* sect. *Patentes* Taxa in Relation to Major Ecological Gradients across Southeastern U.S.A. [a series of charts based on associated woody species]. Posted at <http://www.bluegrasswoodland.com/uploads/Symphyotrichum_patens_complex.pdf>.

Darrach, M.E. 2014. *Lomatium knokei* (Apiaceae), a new, narrowly endemic species from Washington state. Phytoneuron 2014-108: 1–12. Published 1 December 2014. ISSN 2153 733X

LOMATIUM KNOKEI (APIACEAE), A NEW, NARROWLY ENDEMIC SPECIES FROM WASHINGTON STATE

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ABSTRACT

Lomatium knokei Darrach, **sp. nov.**, is a narrowly endemic species of apparent critical conservation concern growing on seasonally wet soils in Kittitas County along the east slope of the Cascade Mountains in central Washington state. The species is distinguished from all other members of the genus by a combination of features of leaf morphology, fruit shape, pedicel length, root characters, and genetic sequencing data. The single known population is confined to three small patches estimated to include a total of an estimated 3000 sparsely to locally densely clustered plants in a vernally wet meadow on South Cle Elum Ridge near the town of Cle Elum. Off-road vehicle threats to the population are serious and ongoing.

Lomatium is by far the largest genus in Apiaceae in North America. Several new species from the USA have been described over the last few years, including *L. ochocense* Helliwell (2010), *L. bentonitum* Carlson & Mansfield (Carlson et al. 2011), *L. pastoralis* D.H.Wagner ex Darrach & Wagner (2012), *L. brunsfeldianum* McNeill (2012), and *L. tarantuloides* Darrach & Hinchliff (2014).

Retired farmer, botanist, and plant collector Donald Knoke, now 94 years of age, of Thorpe, Washington, encountered a species of *Lomatium* with which he was not familiar in a seasonally wet meadow on South Cle Elum ridge in Kittitas County on the east slope of the Cascade Mountains of Washington state in May 2002. The population at this site (type locality) is confined to seasonally inundated deep fine-textured clay loam soils of the colluvial and basalt bedrock derived argixeroll class Hakker Series (WebSoilsSurvey 2014). This site is at approximately 1207 meters on a nearly flat to shallow easterly aspect on the Okanogan-Wenatchee National Forest. Subsequent morphological examination and comparison of specimens with reference material by David Giblin, Mark Darrach, Ben Legler, and other botanists at the Burke Museum Herbarium (WTU), Washington State University (WS), and Oregon State University (OSC, ORE, WILLU) suggested these collections represented a hitherto undescribed species with some morphological similarities to *L. leptocarpum* (Torr. & Gray) Coult. & Rose.

Since its initial discovery, an additional single very small outlier subpopulation along the margins of a seasonally wet meadow approximately 275 meters west of the two main subpopulations was discovered by David Giblin, Peter Zika, and Donald Knoke. The possibility that other sites exist in the general area should be entertained, with particular attention paid to areas with soils in the Hakker Series. Measurements in the description below represent a combination of characters derived from both herbarium material and live plants.

Lomatium knokei M.E. Darrach **sp. nov.** Figures 1 through 7. **TYPE: USA. Washington**. Kittitas Co.: open seasonally wet meadow, 1.87 km ESE of Cle Elum Point, 0.15 km S of FR 3352, 47.136429 N -120.922246 W, common to locally abundant on clay loam substrate, flat or gentle easterly aspects, elev. 1213 m (3979 ft), 20 Jul 2011, *C.E. Hinchliff 1358* (holotype: WTU; isotypes: NY, OSC, RM, UC/JEPS, US, WS,).

Lomatium knokei combines character states distinct from its immediately associated and regionally contiguous congeners and all other recognized members of the genus. The following characters are particularly diagnostic in discriminating between *Lomatium knokei* and other species: plants strict, fruits small and narrowly elliptical on short pedicels, leaves few with ultimate leaflets extremely narrow and generally less than 10 mm in length, younger plants in particular typically with a well-defined small ovoid to elliptical or oblong tuber directly below the root crown.

Herbs: Perennial, long-lived, non-aromatic, glabrous, acaulescent (caulescent), 7.5–35.8 cm in height with typical plants approximately 20 cm in height when in mature fruit. Plant heights increasing approximately 125% from anthesis through to maturity. **Root:** typical specimens (Figure 2) have a small ovoid, ellipsoidal to oblong or turbinate tuber 6.0–15.0 mm broad by 5.0–20 mm in length that becomes a simple or occasionally weakly moniliform taproot distally. Root length 2.0–27.8 cm. Root surmounted by a simple subterranean root crown and a short narrow terete subterranean pseudoscape, 13–43 mm long that is single in all specimens evaluated. Root crown annual scars, when clearly discernable, 3–93 in number reflecting approximate plant age. Typical material approximately 15 years old. **Leaves:** old sheathing leaf bases occasionally present and obscuring up to 25 mm of the root crown, leaves 2–8, most typically 3, venation obscure, glabrous, compound, ternate to biternate-irregularly pinnate, 3.8–17.0 cm wide, 9.1–17.8 cm in length. Petioles 1.4–10.1 cm long with variably developed winged basal portions, winged bases entire, herbaceous with variably green to discontinuously weak to occasionally moderately-developed light purple anthocyanic coloration at the base. Leaf bases becoming stramineous and chartaceous with age, prominent nerves on leaves with winged petioles 6–12. Reduced, ternate irregularly pinnate axillary leaves often present, petioles of these leaves enclosed within broad-winged bases of larger primary leaves, wings lacking or minimally developed, usually entirely lacking nerves. Pressed leaves usually about equally as broad as wide, the leaf outline quadrate, rhombic, or triangular axillary leaves narrowly rhombic. Leaflets spreading, occasionally weakly overlapping, entire, linear-filiform to occasionally very narrowly elliptical, ultimate segments 3–27 mm long with typical values about 10 mm, 0.2–2.3 mm wide with typical values about 1.0 mm. **Inflorescences:** compound, involucre none, numbering up to 6 in the oldest plants, but typically 1 or 2. Peduncles strongly ascending to strict, terete, often weakly and discontinuously anthocyanic at the base. Peduncle length in flower 5.8–19.8 cm with typical specimens around 13 cm, peduncle length in fruit 15.0–36.5 cm with typical values around 23 cm. Peduncles greatly exceeding the leaves as the inflorescence matures with typical increases in peduncle length of approximately 70% at maturity relative to when plants are at anthesis/early fruit. Rays 3–12, unequal in length in flower, grossly so in fruit with increases in longest rays from flower to mature fruit approximately 115%. Minimum ray length per inflorescence in flower 1.0–16.0 mm, maximum ray length per inflorescence in flower 3.7–27.6. Minimum ray length per inflorescence in fruit 1.6–12.0 mm, maximum ray length per inflorescence in fruit 10.7–53.0 mm. Shortest rays usually bearing umbellets with entirely male flowers that do not lengthen with plant maturity. These short, staminate umbellets are frequently somewhat contorted and are clustered at the umbel center, they are irregularly deciduous by maturity and tend to bear fewer flowers. The longer rays bear umbellets that are a mixture of male, female and, to a lesser extent, perfect flowers. Number of rays with entirely male flowers per inflorescence 0–9; typically 2 or 3, number of rays with entirely female flowers per inflorescence 0–7; typically 1 or 2, number of rays with a mix of male, female and perfect flowers per inflorescence 0–9; typically 3 or 4. Male flower pedicels smooth, glabrous, 0.7–2.6 mm in length with typical values about 2.2 mm, female and perfect flower pedicels smooth, glabrous, 0.8–2.2 mm with typical values about 1.2 mm. **Involucel:**

bracts green, herbaceous, narrow to linear, bract number 0–14 with typically values of 5 to 7, distribution radial to irregularly dimidiate. Involucel bracts 1.5–6.4 mm in length, 0.1–0.8 mm in width, glabrous, free to base, often with a well-developed mid-vein, occasionally inserted on flower pedicels. **Flowers:** primarily andromonoecious on most plants, but some plants are polygamo-monoecious, flowers glabrous 6–41 per umbellet with values of 14–20 typically encountered, petals bright yellow, 0.5–1.4 mm long, 0.4–0.9 mm wide, ovate with an adaxially strongly incurved short apiculus; stamens 5 and alternating with the 5 petals, anthers bright yellow to pale yellow, 0.30–0.50 mm by 0.15–0.40 mm, pollen yellow, filaments 0.6–1.4 mm. Stylopodia yellowish green to greenish yellow prior to pollination, becoming reddish purple post-pollination. Styles laterally flattened, 1.5–1.5 mm, strongly curved, outwardly divergent; ovaries green and glabrous. **Fruit:** hemispherically arranged with 0–17 fruit per umbellet; 7 or 8 being the most commonly encountered numbers, the longer rays usually considerably more fecund, pedicels spreading-ascending to semi-erect, 0.8–5.2 mm with typical values of about 2.2 mm encountered on most specimens. Fruits glabrous, 4.0–7.8 mm long with typical material about 6.0 mm in length, 1.6–2.8 mm wide with typical values approximately 2.2 mm. Fruit wing width 0.2–0.5 mm, not obviously thickened, strongly dorsiventrally compressed with rounded base and distal obtuse margin. Fruit aspect ratio 1.91–3.81. Fruit shape elliptical to narrowly elliptical, color greenish tan in the intervals with RGB values ranging from R: 140–212 / G: 115–199 / B: 15–37 (Colorpicker 2014). Dorsal fruit surfaces with 2–4 well-develop nerves flush with the fruit surface; vittae obscure, 4–5 in the intervals, 2 along the commisure, 0 on the wings. **Carpophore:** cleft to the base, persistent. A composite illustration is provided in Figures 1 and 2 and specimen photographs are in Figures 3 through 7.

Paratypes. **Washington**. Kittitas Co.: ca. 200 yards S of FS road 3350, 1.4 mi E of junction with FS road 3350, T19N R15E Sec. 14, N 47° 08.192', W 120 ° 55.329 ', 3350 ft, 8 Jun 2003, *Knoke 304* (WTU), 23 Jun 2003, *Knoke 313* (WTU), 8 Jul 2003, *Knoke 317* (WTU), 11 May 2004, *Knoke 423* (WTU), 8 Jun 2005, *Knoke 753* (WTU), 9 Jun 2007, *Knoke 1303* (WTU); ca. 200 yards S of FS road 3350, N 47.13617, W 120.92193, 1206 m (3956 ft), 22 Jun 2013, *Darrach 1016* (WTU), 13 Jul 2013, *Darrach 1030* (WTU).

Etymology. The epithet "knokei" commemorates the much-respected local botanist and plant explorer Donald Knoke, who initially discovered the populations of the new species and made collections.

Habitat. *Lomatium knokei* is known from a single flat to gentle east-aspect, forb-dominated meadow site on fine-grained clay loam seasonally wet soils of the Hakker Series.

Range. *Lomatium knokei* is presently known only from the type locality with a small outlier subpopulation approximately 275 meters immediately to the west. While comprehensive surveys for the species in the general area have not been conducted and are clearly needed, a GIS soils analysis of approximately 100,000 contiguous hectares clearly indicates the host Hakker Series clay loam soil type is rare throughout the area (Web Soil Survey 2013). If *L. knokei* maintains high fidelity to this soil series, which seems credible, by extension it can be assumed the species is most probably extremely limited in distribution and overall abundance.

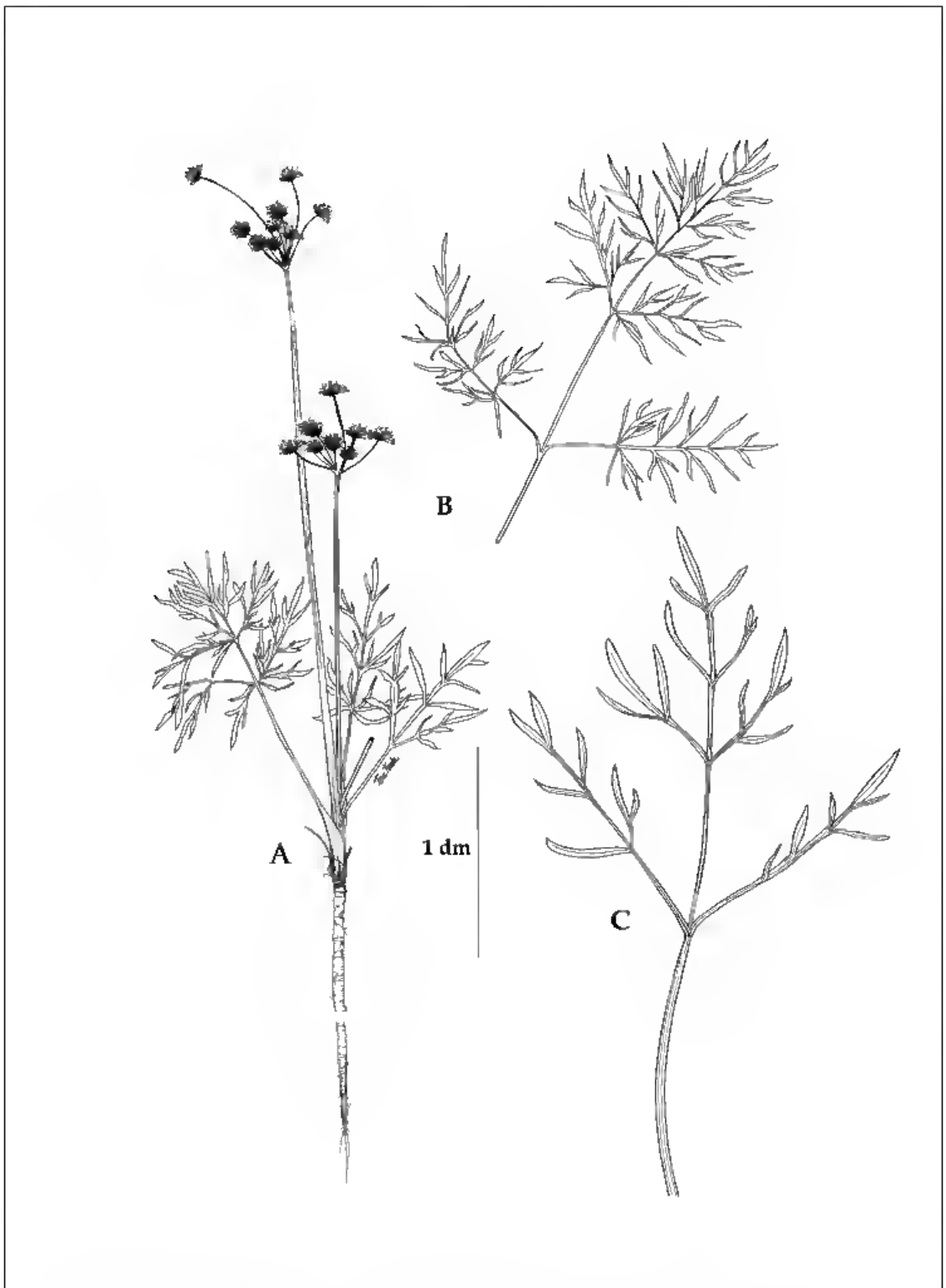

Figure 1 *Lomatium knokei* A Habit of plant with grayed-out segment of infructescence peduncles representing missing segment for illustrative purposes B Primary leaf morphology C Axial leaf morphology

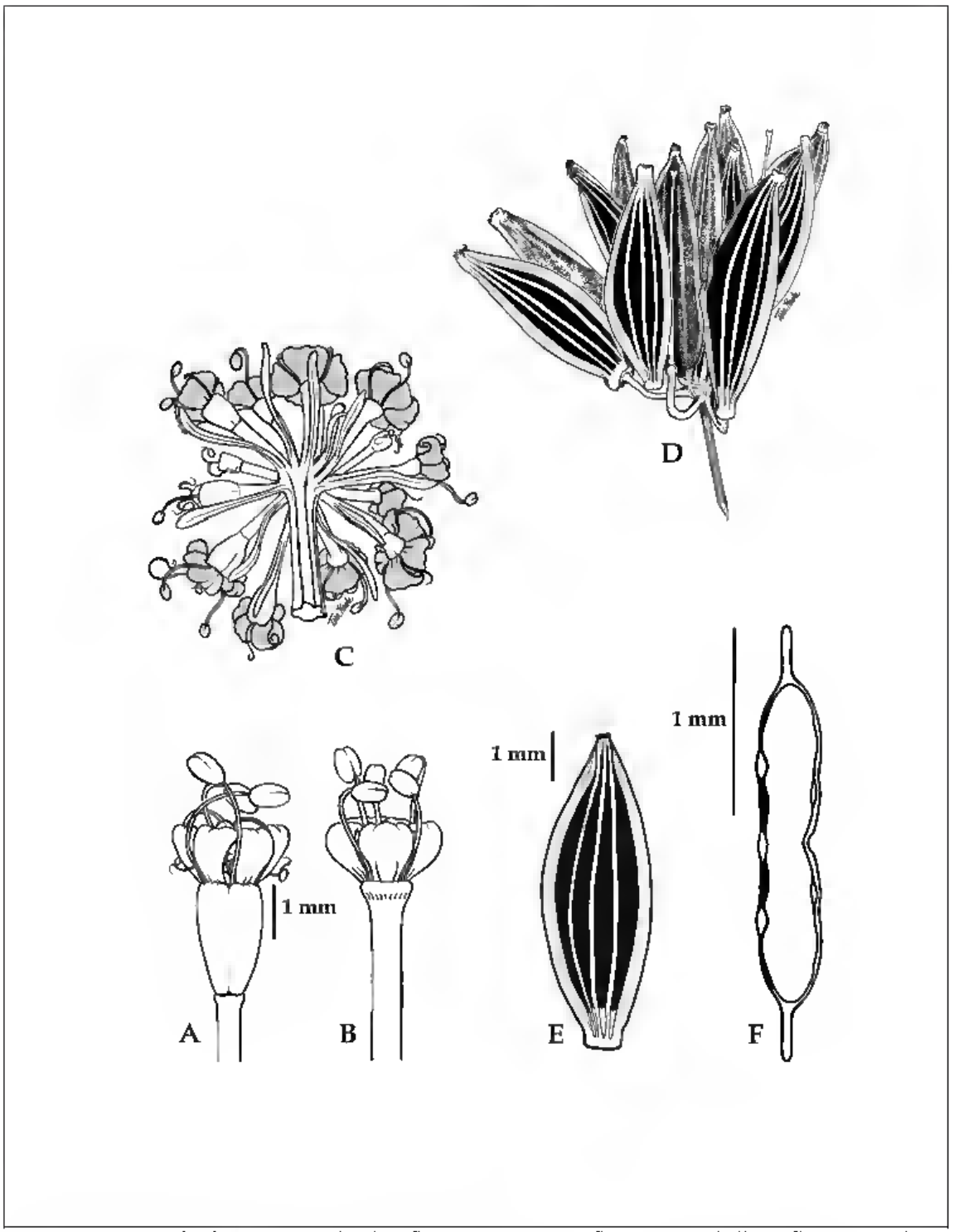

Figure 2 *Lomatium knokei* A Hermaphroditic flower B Staminate flower C Umbellet in flower ventral view with involucel bracts D Umbellet in mature fruit lateral view E Mature fruit F Mature fruit cross sectional view with vittae

Figure 3 *Lomatium knokei* leaves depicting the range of variation of leaf morphology typical for the species Those leaves shown with broad petiole bases are primary while those lacking this feature are axial leaves that arise from inside the broad petiole bases of the primary leaves

Figure 4 *Lomatium knokei* roots depicting the range of variation of morphology typical for the species. Note the tuberous swelling immediately beneath the root crown on the majority of the specimens.

Figure 5 *Lomatium knokei* inflorescence showing well-developed involucel bracts

Figure 6 *Lomatium knokei* maturing infructescence umbellet See illustration for typical scale

Figure 7. *Lomatium knokei* mature plants in situ at anthesis. Plants are approximately 20 to 25 cm in height in this view

Figure 8. *Lomatium knokei* habitat at the type locality

Similarities and relationships

There are recognized morphological similarities between *Lomatium knokei* and other regionally conspecific *Lomatium* taxa. The species with which *L. knokei* is most likely to be confused are *L. leptocarpum*, the recently-described *L. pastoralis* Darrach & Wagner, and *L. tarantuloides* Darrach & Hinchliff (Table 1).

Discriminating Character	*L. knokei*	*L. pastoralis*	*L. tarantuloides*	*L. leptocarpum*
Inflorescence / Infructescence Growth habit	strict	decumbent base and distally ascending to strict	prostrate to weakly ascending	strict
Root Crown Morphology	single pseudoscape, rarely two	usually single pseudoscape	single to multicipital pseudoscape	usually single pseudoscape
Root Morphology	unbranched taproot – usually with small tuber near root crown	unbranched taproot	rarely branched taproot	unbranched irregularly tuberous taproot
Mature Fruit Length	4.0 – 7.8 mm; average value 6.2mm	5.3 – 11.4 mm; average value 7.7mm	3.7 – 8.0 mm; average value 5.4mm	7.0 – 14.9 mm; average value 9.9
Mature Fruit Aspect Ratio	1.91 – 3.81	2.40 – 3.26	1.85 – 4.00	3.32 – 13.33
Flower Color	bright yellow	bright yellow	white (bright yellow)	light yellow
Involucel Bracts	0 – 14; typically about 5 – 7	1 – 12, typically 6 – 8	0 – 8, typically 0	typically 5-9
Leaflet Width	0.2 – 2.3mm, average value approximately 1.0mm	0.8 – 9.7mm, average value approximately 3.5mm	0.4 – 3.8mm; average value approximately 2.0mm	0.3 – 1.7mm; average value approximately 0.9mm

Table 1. Comparison of *Lomatium knokei* with similar species.

Lomatium leptocarpum is readily distinguished from *L. knokei* by its long, narrow nearly sessile fruits with a much higher aspect ratio of approximately 6:1 versus approximately 3:1 for *L. knokei*. *Lomatium leptocarpum* also tends to be a somewhat more robust plant with a greater number of leaves and a larger irregularly moniliform tuberous root. *Lomatium pastoralis* displays markedly decumbent peduncle bases immediately proximal to the root crown, has leaflets that are on average several times more broad than those on *L. knokei*, and has larger fruits. *Lomatium tarantuloides* has prostrate peduncles, fruits that are on average smaller, and usually entirely lacks involucel bracts.

In addition to morphological character separation, a recently published molecular genetic study (George et al. 2014) that included leaf material from a *Lomatium knokei* collection provides additional strong evidence for recognition of *L. knokei* at specific rank. In this broad molecular phylogenetic analysis addressing species-level relationships in the genus, *L. knokei* (recognized with placeholder name "*Lomatium* sp. nov. E" in the publication) is included with strong support in a clade immediately sister to the recently published *L. tarantuloides* (Darrach & Hinchliff 2014).

Phenology, ecology, and conservation

Emergence of *Lomatium knokei* each year occurs primarily as a function of the timing of melt-back of the mountain snow pack. In low precipitation years this may occur as early as April or perhaps, in more typical precipitation years, well into May. Inflorescences are at or near anthesis by early-June in most years and in mid-fruit by late June. The plants rapidly senesce thereafter, seed is generally fully dispersed by mid-July, and the plants become largely unrecognizable as they reach full dormancy.

Lomatium knokei is a long-lived perennial species. Analysis of root crown scars, a proxy for age, indicates that some individuals may approach 100-years old. Typical material collected and analyzed for this publication displayed 10 to 20 root crown scars. It is surmised that older plants reside in areas that may be protected somewhat from herbivory.

The apparent dependence of the vernally wet meadow habitat of *Lomatium knokei* to a well-developed winter snowpack each year suggests impending risks to the type locality population. Nearly all climate models indicate that winter snowpack in the Pacific Northwest in general will become increasingly sparse (Barnett et al. 2005). This scenario argues that the *Lomatium* meadow is likely to become dryer earlier in the season, thus placing pressure on the plants to complete their yearly life cycle in a shorter time — with likely deleterious consequences to population viability.

The species occurs as a single known scattered to dense population of an estimated 3000 individuals on a largely non-forested, vernally wet, gently-sloping meadow substrate where it is a co-dominant species. Peripheral margins of the population include the narrow ecotonal edge of adjoining moist coniferous forest in the Pacific silver fir (*Abies amabilis*) plant association group (Lillybridge et al. 1995). Numerous young plants and seedlings scattered throughout the population suggest that reproductive capacity is not a significant limiting factor in the persistence of the species at the type locality at the present time.

Associated vascular plant taxa documented to co-occur with *Lomatium knokei* include the following: *Abies amabilis, Abies grandis, Achillea millefolium, Antennaria rosea, Camassia quamash, Carex hoodii, Carex microptera, Castilleja miniata, Castilleja tenuis, Deschampsia danthonioides, Epilobium glaberrimum, Erythronium grandiflorum, Fragaria virginiana, Galium* sp., *Geum triflorum, Juncus confusus, Leucanthemum vulgare, Lomatium triternatum* var. *triternatum, Luzula* sp., *Madia glomerata, Moehringia macrophylla, Montia chamissoi, Olsynium douglasii, Orobanche uniflora, Osmorhiza occidentalis, Penstemon procerus, Poa bulbosa, Polygonum polygaloides, Potentilla gracilis, Pseudotsuga menziesii, Pyrrocoma hirta* var. *sonchifolia, Ranunculus uncinatus, Saxifraga nidifica, Senecio integerrimus* var. *exaltatus, Symphoricarpos albus, Taraxacum laevigatum, Taraxacum officinale, Veratrum californicum, Wyethia amplexicaulis,* and *Trifolium* sp.

Field observations within the population indicate that *Lomatium knokei* plants can be, at least periodically, significantly impacted by insect herbivory. Both aphids and minor instances of galling insects have been noted. Aphids in particular have been notably abundant in both the 2013 and the 2014 field seasons. While other instances of insect herbivory in the genus have been noted (Thompson 1998), it is this author's experience that it is atypical in the genus as a whole; likely owing to the general preponderance of inhibitory secondary chemicals so prevalent in many of the species (Asuming et al. 2005).

An additional factor imparting a salient threat to the existence of the species at the type locality is the prevalence of illegal off-road vehicle activities. An unauthorized road is at present being used by 4-wheel drive enthusiasts. It cuts directly through the population and plants are clearly being destroyed accordingly.

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UTRICULARIA CORNUTA (LENTIBULARIACEAE) NEW TO THE ARKANSAS AND OKLAHOMA FLORA

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ABSTRACT

Utricularia cornuta is documented as new to the flora of Arkansas and Oklahoma. It is known from the West Gulf Coastal Plain by one collection from Calhoun County, Arkansas, and one collection from Pushmataha County, Oklahoma, apparently at the northwestern edge of the distribution of the species. The Arkansas collection was made summer of 2004 and Oklahoma collection during the summer of 2014.

Utricularia cornuta Michx. (Lentibulariaceae), commonly called horned bladderwort, is an annual to perennial aquatic or terrestrial wetland plant bearing bladders for capturing minute animal life. The plant is terrestrial, usually in nutrient-poor peat or moist sand, or aquatic in floating mats. The flowering stems (scapes) are erect, numerous, to about 35 cm tall, with few scale-like bracts, and 1–9 yellowish, 2-lipped flowers near the summit. Plants flower from May to September. The species is widely distributed in the eastern USA and Canada — it is most abundant along the Gulf Coast and southern Atlantic coast and from Minnesota across the Great Lake region to Maine, but apparently rare elsewhere (USDA, NRCS 2014; Kartesz 2014).

Utricularia cornuta in reference to the flora of Arkansas is neither included in the Annotated List of the Vascular Plants of Arkansas (Smith 1988) or Keys to the Vascular Plants of Arkansas (Smith 1994). In The PLANTS Database (USDA, NRCS 2014), *Utricularia cornuta* is referenced as native to the state of Arkansas but without county location and apparently without supporting data (a specimen citation or reference to one). It is mapped for Calhoun County in Gentry et al. (2014) and Kartez (2014) on the basis of the specimens cited below, but no information is provided aside from the county-level distribution. *Utricularia cornuta* in reference to the flora of Oklahoma is included neither in the Keys to the Flora of Oklahoma (Waterfall 1966), Checklist of the Flora of Oklahoma (Taylor and Taylor 1994), Oklahoma Vascular Plants Database (Hoagland et al. 2004), Keys and

Descriptions for the Vascular Plants of Oklahoma (Tyrl et al. 2010), The PLANTS Database (USDA, NRCS 2014), nor The Biota of North America Program (Kartesz 2014).

Based upon specimens cited below, *Utricularia cornuta* may now be documented as part of the flora of Arkansas and Oklahoma.

Voucher specimens. **USA. Arkansas.** Calhoun Co.: 3.3 mi. SW of Harrell, W of CR 116 and S of gas pipeline right-of-way, within abandoned railroad right-of-way, vicinity of 33°28'12.00" N, 92°25'54.01" W (Artesian 7.5' quadrangle), 15 May 2004, *Witsell 04-0397* (with Pagan, Sundell, Pelton, Amason) (ANHC); same date and location, *Sundell 16,935B* (with Pagan, Witsell, Pelton, Amason) (UAM) (Figure 3). **Oklahoma.** Pushmataha Co.: Junction of Indian Nation Turnpike and OK Hwy 3, ca. 0.3 mi N of junction of Indian Nation Turnpike/OK Hwy 3, E side, 0.4 mi N of the jct. of OK Hwy 3 and Indian Nation Turnpike on Indian Nation Turnpike in hillside bog in right-of-way on the E side of Indian Nation Turnpike (34°14'25.78" N, 95°39'8.95" W), 9 Aug 2014, *J. Singhurst 20,830* with L., A., and R. Singhurst (BAYLU, OKL). Figures 1 and 2.

The nearest documented occurrences of *Utricularia cornuta* to the reported Arkansas site is 210 km to the south in Natchitoches Parish, Louisiana (Thomas & Allen 1998) and 180 km to the southwest at Caddo Lake, Marion County, Texas (*Singhurst, Adams, and Fitch 15358B*, BAYLU). The record nearest to the Oklahoma site is 155 km south to Wood County, Texas (*Holmes and Singhurst 12917* and *12917*, BAYLU). The Arkansas and Oklahoma occurrences apparently represent the northwestern limits of the distribution of the species.

Figure 1. Hillside bog with *Utricularia cornuta* in Pushmataha County, Oklahoma. Photo by Jason Singhurst.

In Calhoun County, Arkansas, *Utricularia cornuta* occurred scattered patches over an 0.5 × 3 meter area on wet mineral soils in an open herbaceous seepage wetland at the topographic break between the "Intermediate Terrace" and "Prairie Terrace" geomorphic surfaces of the Pleistocene Fluvial Terraces (EPA Level IV) Ecoregion (a series of ancient terraces of the Saline and Ouachita Rivers). Seven plants of *U. cornuta* were observed in full flower. Associated species include *Cyperus haspan*, *Dichanthelium scabriusculum*, *Doellingeria sericocarpoides*, *Eleocharis tortilis*, *Eriocaulon decangulare*, *Eryngium integrifolium*, *Eupatorium rotundifolium*, *Fuirena bushii*, *Helianthus angustifolius*, *Juncus* spp., *Lycopodiella appressa*, *Mitreola sessilifolia*, *Myrica heterophylla*, *Osmunda regalis*, *Paspalum laeve*, *Paspalum praecox*, *Platanthera cristata*, *Pluchea foetida*, *Polygala nana*, *Pseudolycopodiella caroliniana*, *Rhexia mariana*, *R. virginica*, *Rhynchospora glomerata*, *R. gracilenta*, *R. inexpansa*, *R. rariflora*, *Scleria muehlenbergii*, *Sisyrinchium atlanticum*, *Sphagnum* spp., *Utricularia gibba*, *Woodwardia areolata*, *Woodwardia virginica*, *Xyris ambigua*, *Xyris baldwiniana*, and *Xyris torta*.

In Pushmataha County, *Utricularia cornuta* appears restricted to Oklahoma Acidic Hillside Seeps (Nature Serve 2014) surrounded by the Antlers Sand Formation. These hillside seeps are highly localized and isolated wetlands in southeast Oklahoma that include a number of disjunct West Gulf Coastal Plain flora at their northwest range limits. Oklahoma Acidic Hillside Seep dominant species include *Andropogon virginicus*, *Dichanthelium scoparium*, *Boehmeria cylindrica*, *Sphagnum* spp., and *Polytrichum commune*. Other characteristic flora of the two hillside seeps include *Baccharis halimifolia*, *Drosera brevifolia*, *Carex* spp., *Cyperus strigosus*, *Eleocharis tortilis*, *Eriocaulon decangulare*, *Eupatorium perfoliatum*, *E. rotundifolium*, *Gratiola pilosa*, *Hydrolea ovata*, *Juncus validus*, *Helianthus angustifolius*, *Lycopodiella appressa*, *Ludwigia hirtella*, *Mitreola petiolata*, *Osmunda cinnamomea*, *O. regalis*, *Oxypolis rigidior*, *Pluchea foetida*, *Rhexia mariana*, *R. virginica*, *Rhynchospora caduca*, *R. gracilenta*, *R. rariflora*, *Rubus argutus*, *Scleria sp.*, *Utricularia juncea*, *U. subulata*, *Xyris difformis*, and *X. jupicai*. The *U. cornuta* population is restricted to a 1 m x 1 meter patch along a perennial seep run.

Figure 2. *Utricularia cornuta* in hillside bog in Pushmataha County, Oklahoma. Photo by Jason Singhurst.

Figure 3. Photo of lower lip with a prominent, downward pointing spur of *Utricularia cornuta* in Calhoun County, Arkansas. Photo by John Pelton, 15 May 2004.

Utricularia cornuta is ranked S1 by the Arkansas Natural Heritage Program and will be ranked S1 by the Oklahoma Natural Heritage Inventory, indicating that it is "critically imperiled in the state because of extreme rarity or because of some factor(s) such as very steep declines in populations making it especially vulnerable to extirpation from the jurisdiction" (Arkansas Natural Heritage Commission (2014), Oklahoma Natural Heritage Inventory (2014), and NatureServe Explorer (2014).

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RESPONSE TO A PARTICULARLY NASTY REVIEW IN THE JOURNAL *CLADISTICS*

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ABSTRACT

An outrageous book review in the journal Cladistics by A.V.Z. Brower of "Framework for Post-Phylogenetic Systematics" by R.H. Zander lacks understanding and collegial dignity. Examples of unpleasantries and of errors of fact and logic by the reviewer are noted here. And although I have attempted a light-hearted response, this indulgent and kindly rebuttal was rejected by the editors of Cladistics. It is offered here anyway, given that there are several new and potentially important observations that warrant publication. Topics discussed in this rebuttal are identification of paternal ancestors, uncertainty in road closings, virtual storks, correctly uncertain accuracy versus wrongly certain precision, shared and serial ancestry, classical rules of thumb, and taking the fight for reason to the barricades. Paraphyly is the best friend of molecular systematics.

The review (Brower 2014) of my recently published "Framework for Post-Phylogenetic Systematics" (Zander 2013) is exactly what I expected! Cladists are famous for their derisive disapprobation of classical evolutionary systematics. Let's extract a few representative disparagements: "retrogressive," "authoritative bleating," "browbeaten," "militantly entrenched," "reactionary intransigence," "schismatic," "calumnies," "preposterous," "sentimentally favored paraphyletic groups," "spinning of scenarios," "nihilistic," "preconceived notions," "brass," "numerological justification," and, last but not least, "Zander would like to return to a pre-cladistic world where … perhaps he is not a monkey." Wow! This justifies a civilized, collegial, measured response that untangles misunderstandings.

Because I feel that future progress in theoretical systematics shall come from students, not sunk-cost-attentive, established phylogeneticists, I ask if those considering a career in systematics would want to join a group replacing discursive logic and collegial colloquy with True Believer sloganeering and personal obloquy. My book demonstrated, in my opinion, certain fatal flaws with cladistics and phylogenetics, and these should have been addressed by the reviewer, but they were not. I wrote, for instance, on p. 123 that "cladistics alone cannot determine monophyly" and in my opinion justified that comment, but there was no reasoned reply from the reviewer. This may be because standard evolutionary theory relevant to classification is process-based and involves both shared and serial ancestry, while cladistics uses only pattern-based evidence of sister-group relationships. The two approaches, though partially compatible, usually talk past each other.

In opposition to the reviewer's reproach, I do know what cladistic analysis is, having been a fifth columnist for many years, learning hidden secrets. Cladistics is derived from phenetics and thus is also an optimally dichotomous method of optimal sorting, but it uses trait transformations on a non-ultrametric tree plus outgroup selection to root the tree. This is fine, so far. Then the result, which so appealingly looks like a natural key, is turned upside down and passed off as an evolutionary tree! No, wait, it is not called that, but instead a cladogram or phylogenetic tree. This is because many of the early cladists knew perfectly well that evolution is not essentially dichotomous (but now this important knowledge has been lost to science). The result is at best a diagram of shared descent and should be modified by what

information is available about serial descent. One would not base a supposedly evolutionary classification on just shared descent, would one? Or would one?

Cladograms are the raw results of the optimally dichotomous sorting by the cladistic analytic method. A "cladogram" is thus defined as "not an evolutionary tree." Ditto for a phylogenetic tree. The relationships between the taxa analyzed are "phylogenetic relationships" not evolutionary relationships. Classification is now much affected by the cladistic method of analysis, and taxonomic names are not changed, added, or deleted to reflect new evolutionary information but to reflect new cladistic information. My book attempts to remedy this by introducing polychotomous natural keys from which *evolutionary* trees can be constructed.

Also, contrary to the reviewer's denouncement, I really do understand the difference between cladistics and phylogenetics, but I lump them (let's call the two "phylocladistics") for the same reason that sensible people lump creationism and intelligent design — they both have wrong assumptions, faulty logic, and shore up selected facts with attractive but false simplifications. For example: Evolutionary systematics, to make a cogent analogy, would produce a diagram "Al → Bob" because after a trait-transformation clustering of OTUs (in this case examining census data), we also infer from non-sister-group-informative data (birth certificates) that Al is the father of Bob. Cladists make do with just "(Al, Bob)" and call this parenthetic diagram (in the context of a larger cladogram) a representation of monophyly even though no direct ancestor-descendent relationship is presented. Phylogeneticists are more demanding, however, and insist on the model "unknown shared ancestor → (Al, Bob)."

Evolutionary systematists can infer who their immediate patristic ancestors are, which, in the case of Bob, is "Al." Cladists apparently do not care, and phylogeneticists are confused, assuming, possibly, a stork? This analogy, though intraspecific, is demonstrative of the relationships promoted by the three schools of systematics. The reviewer asserts that "spinning of scenarios"… requires "knowledge of relationships independent of the evidence in the data matrix." Science, however, deals with inferences from relevant data, and inferences from restricted data must be expected to give less than relevant results. Clearly, diagrams or models in evolutionary systematics incorporate much more evolutionarily relevant information than do those of cladistics or phylogenetics. We evolutionary systematists consider serial transformations in monophyletic groups the basic process-based feature of evolutionary analysis.

The preoccupation of cladists is to find the shortest tree. If there are two or more descendant taxa from one extant ancestral taxon, then, reasonably, a longer tree is required. Cladists' zeal is misdirected, and maximum parsimony actually masks multiple serial transformations such as bursts of adaptive radiation from a single ancestral taxon. Phylogeneticists have somewhat the same preoccupation but additionally contend over whether it was the same or different storks that brought Al and Bob. There are no storkish ad hoc inventions in caulograms or Besseyan cacti of serial macroevolutionary transformations, although the postulation of unknown ancestral taxa is acceptable when justified by inference (not as a structural part of the phylogenetic method).

The reviewer avers that support for clades should be empirical, not warm and fuzzy group favoritism. So, another analogy: Consider a salesman who wants to visit several cities by the shortest route and needs to know how much money to take for gasoline. The optimal route is the solution to the classical traveling salesman problem, and support for the shortest route may be based solely on distances (how much better the shortest route is than the next shortest, and so on). Thus, support is measured by information already in the data set. But suppose information not relevant to the distance between cities is also available, for instance, roads connecting various cities are sometimes closed when you show up in your car but you know what the probability of closure is for each road and you thus know which roads to avoid. Optimality judged only from the data set on road lengths can be more *precise* than total evidence involving uncertainty with other information, but *accuracy* based on total evidence can be critical in

decisions even when there is more uncertainty when all data are examined. Cladograms are precise but you can run out of gas.

The reviewer complains about my "downweighting of the empirical evidence." Scientific theories must address all evidence, including that which is not in the cladistic data set. Yes, they must. Eliminating evidence for serial ancestry does not make sister-group evidence the only empirical evidence available. Scientific inference using induction and analogy does not result in "preconceived notions" but along with deduction can help develop a process-based theory of evolutionary transformation that results in a better, testable classification that predicts where new taxa will fit into the theory.

The reviewer asserts that I offer "a method for differentiating (morpho)species in terms of the geometric mean and Fibonacci series." No such thing. I suggested instead that classical taxonomists have used such as a part of a heuristic method for writing descriptions for many years, not realizing the fundamental physical and mathematical reason for their doing so. Powerful and useful heuristics underlie the methods of classical systematics.

It has been said that, in long-running listserver arguments between systematists, eventually someone calls someone else a Nazi. I would never do this. Instead, I have devised a 10-degree Scale of Evil. The Scale is exponential, as in the Richter Scale (base 10). As with earthquakes, a three is the minimum detectable event of evil, rarely very damaging, such as turning your head from an instance of social injustice, not giving a beggar a buck when you probably should have, or hurting someone's feelings and not fixing it. Four to 4.9 is light damage, 5 to 5.9 is moderate with few casualties, 6 to 6.9 is strong with up to 25,000 dead, 7 to 7.9 is major with up to 250,000 dead, 8 to 8.9 is great with large cities decimated, and 9 or more is total destruction. A ten would be a paper I found by A. Hitler (no citation to protect innocent minds) vigorously defending brutality in service of the state.

Are major cladistic classification changes that are due to avoidance of paraphyly and implementation of strict phylogenetic monophyly truly harmless? Or perhaps shall they have a high rating on the Scale of Evil for elimination of inferable ancestor-descendant relationships? Should we classify the polar bear as a brown bear, or not? Is a cactus just another portulaca? Celebrity species can be dealt with case by case, but there are myriad small, less well-known families, genera, and species that have fallen to epistemological extinction due to misplacement, or synonymization, or crowded into anonymity among a number of new, trivial molecular or cryptic families, genera, and species. The specialist reader can doubtless name some, and he should assess damage and raise a squawk.

In my own case, the moss family Pottiaceae of 76 genera that I've studied for 50 years has had three related families involving three genera dumped into it by molecular systematists, another two genera excised to a new family, one genus buried in another, and another genus split into four, all due to a desire to eliminate paraphyly in molecular cladograms. Although occasionally minor morphological traits are trotted out that appear to support such classification changes, no support is possible from morphological traits that cannot together stand on their own in distinguishing taxa, particularly when another explanation of the molecular paraphyly is possible, namely serial descent. Conversely, no molecular classification can falsify a morphological one unless it itself can stand alone (without morphological input), which presently is laughable, given poor sampling and no islands of stability in a sea of cladogram branches. Given that a cladistic earthquake affected nine of the 76 genera of Pottiaceae, this is clearly more than a few casualties, and I can easily assign a 6.5 on the Scale of Evil for that large family, and a 10 for each of the three blasted smaller families. Readers may wish to rate their own groups of specialization as to the effect of strict phylogenetic monophyly in destroying, inventing, or displacement of taxa, perhaps on a similar Scale, or alternatively, use a Holophyletic Scale of Truth and Light if they have the brass.

The reviewer "found it tiresome to be browbeaten with redundant claims about the supposed shortcomings of molecular systematics … ." Ridiculous. I pointed out clearly that molecular systematics has introduced two quite powerful analytic tools: (a) distance on a cladogram greater than expected extinct paraphyly, and (b) known paraphyly interpretable as an ancestor-descendant relationship. Paraphyly is the best and perhaps only friend of molecular analysis. Everything else, of course, either reflects preselection of OTUs with known classical relationships or may be considered aleatory.

"Zander frequently repeats his arguments, sometimes almost verbatim and at length." Exactly. This is justified in the Introduction in that the catharsis needed for deprogramming is facilitated by repetition, shame, and appeals to reason. "Zander is one of a small group [of] militantly entrenched advocates of paraphyly … ." The advocates of evolutionary systematics, I might remind the reviewer, are a small group only if they are narrowly defined as paraphyly-huggers. Most practicing taxonomists do alpha taxonomy without any particular investment in cladistics or phylogenetics, but I do get occasional thanks from them for taking the fight for reason to the barricades. I have noted, in addition, a general unease or even cynicism among classical botanists when I inquire if they were ever asked to vote as to whether their institution's herbaria are to be re-ordered according to the latest APG phylogenetic classification or be arranged by some more sensible system like an updated version of that of Thorne or Takhtajan.

The reviewer asserted that "a book review is not the forum for a full-fledged refutation of a schismatic research programme." Why not? I made only a few major suggestions of how to fix systematics by combining the best of classical, cladistic, and phylogenetic methods. Such is only schismatic if all systematists were cladists now, which is an arrogant conceit on the part of cladists that one reads often in the literature. The reviewer carefully avoided substantive criticism of my emphasis on process-based causal theory, heterophyletic inference of deep ancestors, self-nesting ladders, superoptimization, treating heuristics as powerful analytic tools based on physics, treating the genus as a basic unit of evolution, and the danger to conservation and biodiversity research of classifications based only on sister-group analysis. Surely the reader would like some rational evaluation of these from the reviewer.

I have had as much satisfaction in writing this response as the reviewer doubtless had in crafting his acerbic review. The issues, however, are serious. Changes made in classifications have been considered of little consequence because classifications are easily modified if wrong. But in the context of the need for scientific guidance during a world extinction event, wrong though potentially corrigible classifications, even if ephemeral, can greatly affect conservation planning, triage, political decisions, and scientific evaluations of biodiversity.

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REPLY TO C. DAVID BERTELSEN: REVIEW OF PLANT ELEVATION CHANGES IN ARIZONA

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David Bertelsen recently published an essay (Bertelsen 2014) discussing some methodological aspects of plant ecology. The methods he addressed have long been debated in the ecological literature and there is no need to comment on them here. However, his essay also critiqued our recent paper on plant distributions and climate change in the Santa Catalina Mountains (Brusca et al. 2014) and, incidentally, also the work of Robert Whittaker and William Niering (Whittaker & Niering 1964; Whittaker 1967). We feel that Mr. Bertelsen's summary of our paper was inaccurate and misleading, and we take this opportunity to correct his misunderstanding of our work.

Much of Bertelsen's essay faults us for giving evidence of plant elevational range distributions in the Santa Catalina Mountains that he feels are inaccurate for that mountain range. We are well aware of Bertelsen's many years of hiking Finger Rock Trail in the Santa Catalinas, recording changes in plant phenology across multiple habitats. However, his observational approach has little to do with our own, which was strictly to test a specific hypothesis. Our objective was to empirically test patterns predicted by models that suggest that upslope movements of plants are already underway. Because our questions and hypotheses focused solely on species elevation ranges, as do the models and Whittaker and Niering's publications upon which we are basing our comparisons, we do not require, as Bertelsen states, an understanding of where core and peripheral

populations reside. Our statistical analyses clearly support the dominate patterns in species range changes over the past 5 decades along this transect, which are (1) upslope shifts in their lower elevation range and (2) contracted elevational ranges. While this does not apply to all the species we studied, the majority of the species whose range differed from Whittaker and Niering (1964; hereafter W&N) showed upslope shifts in their lower elevation range (52%) and range contractions (59%). Compare this to only three species (11%) that had range expansions, two of which increased their elevational range, a pattern consistent with increasing temperatures at higher elevations.

Thus our goal was not to describe plant diversity in this mountain range. Our study was designed to repeat a single transect line, the 1963 W&N "Catalina Highway Transect." We made no claims that this transect should be viewed as representative of the entirety of the Santa Catalina Mountains. It is obvious that plant elevational ranges differ by location throughout the range, depending on many factors. To claim that we introduced "significant sampling bias" by not sampling riparian/wet canyon sites is to completely miss the point of our study. We attempted to find the best possible way to compare the admittedly poorly documented W&N data to current-day plant distributions, and thus we chose to use only the best W&N dataset, upland sites along their well-known Catalina Highway Transect. Of course, as Bertelsen notes, diversity in riparian habitats is often greater than in upland sites, but that was simply not the focus of our study. Bertelsen's observation that other researchers have reported alligator juniper from other elevations (e.g., Sabino Canyon) than those reported in our paper are irrelevant, because those were not from the W&N transect line. Alligator juniper has been reported by many other workers throughout the Catalina Mountains (e.g., Niering & Lowe 1984, from 3500 ft), but these other records were not from upland sites along the Catalina Highway Transect and so they have no bearing on our study.

Recently, Brian Enquist (University of Arizona) produced an interactive niche-model-based tree distribution predictor (Enquist 2014) that allows users to graphically visualize the effects of differ climate change scenarios on nearly a hundred tree species over time. We recommend this visual tool for those interested in climate effects on Southwestern montane ecosystems. A click on alligator juniper under different climate change scenarios is quite revealing.

The criticism that our plots were "near the heavily traveled [Catalina] Highway" and that this could have led to effects on plant distributions ignores the methodological protocols we used and described in our paper. Our plots were all 0.25 – 0.75 km from the highway, in rugged, steep terrain. We saw no evidence whatsoever of significant human impact in these areas, nor were they accessible to vehicles or road crews, etc., as Bertelsen claims Further, this was the same highway transect line used by W&N in 1963, and that was the sole source of our comparison.

Bertelsen claims that we compared our data to 34 of the W&N "plots," but that is incorrect. As we noted in our paper, we compared our data to the 30 plots shown in their Catalina Hwy transect diagram (Fig. 1, p. 10) that were upland (non-riparian/wet canyon) montane (3500-9000 ft elevation) sites. This figure is a graphical representation of the large W&N data table in the same paper, and the sites that were used for comparison are listed in the table (p. 15) as "elevation belts" III through VIII along the Catalina Highway, excluding "deeper ravines or canyons with flowing streams." To get the 34 points in this graph that Bertelsen apparently counted, one would need to include the 4 "Canyon Forest/Ravine" sites, which we specifically excluded (because we focused only on upland sites).

Bertelsen claims we did not include "non-occurrence" data, but this is incorrect. Complete lists of all plant species from every transect were cited (Moore et al. 2013), and these lists provide evidence of occurrence/non-occurrence for the 27 species we reported on.

Bertelsen faults us for not collecting voucher specimens. However, all 27 of the species we identified and counted are large well-known perennials, from trees to large shrubs that any competent naturalist could easily identify. And they were the most common plants in our plots. Nearly half of the species were conifers, oaks, and large perennial shrubs (well-tested field keys to southern Arizona conifers and oaks can be found at <http://rickbrusca.com/http___www.rickbrusca.com_index.html/Research.html>). As we stated in our paper, "It is worth noting that even a casual observer could recognize the changes in plant elevation boundaries since the W&N surveys of 50 years ago — without so much as stopping the car as they drive up the Catalina Highway. Large and conspicuous plants such as alligator juniper, bracken fern, beargrass, and sotol simply do not begin to appear [along the highway] until much higher elevations than reported by W&N in 1964." Large, obvious and widely distributed species such as pines, firs, oaks, alligator juniper, bracken fern, and bear grass cannot be easily mistaken for anything else in the Santa Catalina Mountains. Furthermore, the lead botanist on our plot surveys was John F. Wiens, author/reviser of the standard botanical reference for Arizona (*Plants of Arizona, 2nd ed*).

Bertelsen criticizes the lack of georeferencing, specific elevations, and other associated data in the original W&N dataset. As we addressed in our paper, this is a challenging aspect of working with old datasets — the W&N fieldwork was done long before the advent of GPS or even desktop computers. But these data can also be rare goldmines of important information, and Whittaker's 50-yr old Catalina Highway Transect has always been regarded as a pioneering cornerstone in American plant ecology. We compensated for lack of georeferenced and point-elevation data in the W&N dataset in numerous ways, including not recognizing an elevation shift unless our data fell entirely outside the 1000 ft elevation band used by W&N. This highly conservative approach potentially greatly underestimated elevation change in species since 1963. For example, if the W&N data recorded the lower elevation boundary for a species as 4000-5000 ft and our data record the lower elevation boundary of that species at 5100 ft, we recognize only a +100 ft elevation shift, even though the actual shift could be as much as 1100 ft. We also restricted our analysis to common species in order to avoid possible sampling errors with rare species. Furthermore, our sample plots were separated from one another (on average) by just 50 m in elevation, and species showing upslope movement of lower elevation had an average gain of nearly 160 m — more than three times our elevation sampling breaks — further indicating that our sampling effort was adequate.

Bertelsen points out that "correlation does not imply causation," which is of course true. However, we made no claim of specific causation in our study. We simply tested the hypothesis, based on modeling studies, that warming and drying climates are driving plant species up mountain slopes, and we found that on one transect line in one mountain range in Arizona that these factors (rising air temperatures, declining precipitation, and changing plant elevation ranges) were correlated, thereby supporting/not falsifying the prediction. The importance of this study lay in the 50-year old data set that was available from the historical work of Robert Whittaker — an historical record rarely available for field studies.

The last sentence of Bertelsen's essay is perhaps the most curious of all. It states that "With any degree of certainty, we can only say that short-term change in one response over a few decades is consistent with what we might expect with a changing climate." This is precisely the same conclusion drawn from our study.

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NOTEWORTHY COLLECTION OF *PAPAVER RHOEAS* FROM INDIANA

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ABSTRACT

A new county record of *Papaver rhoeas* is reported in Allen County, Indiana. Voucher specimens have been deposited in the Indiana University-Purdue University Fort Wayne herbarium. Due to the location, a protected mesic prairie under active management, and the increasing number of county records in Indiana, there may be concern regarding this species collection.

Specimens of *Papaver rhoeas* L. (Papaveraceae) were collected in Allen County, Indiana, within Eagle Marsh Nature Preserve, which is protected and managed by Little River Wetlands Project (LRWP). Much of the property under LRWP management has undergone extensive activities to promote establishment of native plants within wet to mesic prairies, in addition to native tree and shrub plantings in drier areas (Cunningham et al. 2014). While the occurrence of *P. rhoeas* may be relatively rare, the number of encounters have increased recently in Indiana. The collection of this species in Allen County, is of importance due to the managed area it was found, which is dominated by native species, and because it is a new county record of occurrence.

Papaver rhoeas has a spotty distribution across much of North America (Gleason & Cronquist 1991; Kartesz 2014). In Indiana specifically, its occurrrence has been cited in five counties in the southern portion of the state (Jackson, Lawrence, Perry, Pike, and Ripley), as well as two counties in the far north (LaGrange and St. Joseph) (Kartesz 2014). Other county records missing from distribution descriptions include Henry and Jasper counties (Ruch et al. 2002; Overlease & Overlease 2007). Deam (1940) mentioned *P. rhoeas*, implying it was minor in occurrence in Indiana without listing any county locations; likely escaped from gardens similar to locations in southern Michigan (Nieuwland 1914). However, other exhaustive lists of Indiana plants omit *P. rhoeas* (Crovello et al. 1983). A recent bioblitz of Eagle Marsh Nature Preserve occurred on 31 May 2014 in an effort to identify all biota within the property, but *P. rhoeas* was not encountered (unpublished data).

Voucher specimens. **Indiana**. Allen Co.: Eagle Marsh Nature Preserve, near the boundary of the preserve neighboring a paved bike path, 41°02.24' N, 85°14.30' W, 14 Sep 2014, *Marshall LRWP001, LRWP002, LRWP003* (Indiana University-Purdue University Fort Wayne Herbarium).

At the collection locality, three groupings of plants were found approximately 10-15 m apart with 6-10 individuals in each group. While each plant had slight variations in the typical characteristics found in *Papaver rhoeas* flowers (Fig. 1) — they all produced peduncles with spreading-hispid pubescence and a glabrous subglobose capsule. These characteristics separate *P. rhoeas* from *P. dubium* L., which has a much more obovoid capsule and appressed pubescence, and from *P. somniferum* L., the stem of which is glabrous (Gleason & Cronquist 1991; Kiger & Murray 1997).

Much of the work investigating the invasion potential of *Papaver rhoeas* has occurred in Europe (e.g., Chancellor 1985; Guillerm et al. 1990). While *P. rhoeas* is often described as being

Figure 1. *Papaver rhoeas*. (A) Typical floral characteristics: blue anthers and dark spots at base of petals. (B) Common variant lacking typical dark spot.

limited to waste areas (Voss 1985), there is potential for it to have an impact in agriculture (Wilson & Wright 1990; Wilson et al. 1995). Eagle Marsh Nature Preserve is actively managed, typically with fire and mowing (personal observations). While such disturbances could potentially provide pathways for *P. rhoeas* to colonize farther into the property, there is evidence that it is a fairly poor competitor compared to other annual plants (Goldberg & Fleetwood 1987; Torra & Recasens 2008). Unfortunately, the combinations of seed bank development in mesic soils with intermittent disturbance, including mowing and fire, may provide suitable habitat for *P. rhoeas* invasion and competition (Baskin et al. 2002; Trabaud 2002; Cirujeda et al. 2006; Ellenberg & Leuschner 2010).

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A NEW SUBSPECIES OF *SIDALCEA HICKMANII* FROM OREGON

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ABSTRACT

Sidalcea hickmanii subsp. **petraea** S.R. Hill & R. Halse, **subsp. nov.**, is described from Jackson County in southwestern Oregon. It is the only representative of the otherwise Californian *Sidalcea hickmanii* in Oregon and is the northernmost of the seven subspecies known. All are local endemics thought to be isolated remnants of a previously more widespread species. The new subspecies differs from the other subspecies in its predominantly white flowers and by the predominance of 2, rather than the more typical 3, involucellar bractlets. It is a several-stemmed perennial with congested spicate racemes, and it is known from a single location, Neil Rock.

An entry for a new subspecies of *Sidalcea hickmanii* Greene in Oregon was included on the Oregon Natural Heritage Program February 2001 list as *S. hickmanii* subsp. nov. (ONHP 2001). This was of particular interest to Hill because he was in the process of writing the treatment for North American *Sidalcea* for the Flora North America, Vol. 6 (in edit), and to Halse because he was compiling a list of all of the Oregon species of *Sidalcea* and *S. hickmanii* was not previously known for the state.

The ONHP listing was based upon the first collections of this plant, from the top of Neil Rock in southern Oregon. The first known collection of the plant was made 25 June 1998 by Marcia Wineteer of the Medford District Bureau of Land Management [BLM], and the second was made 13 June 2003 also by Wineteer. The 2003 collection was sent by the BLM to Halse in 2007, who identified it as *Sidalcea hickmanii* and recognized it as a possible new subspecies of that taxon, but it was an incomplete specimen and not suitable for a full description. On 13 June 2003 the plant was in early flower and the inflorescence was somewhat immature. The specimen was pistillate with non-functional anthers on one stem of the collection, and the other (unconnected) stems had bisexual flowers. In March 2008 the specimen was brought to the attention of Hill, who was in the process of describing two new subspecies of *S. hickmanii* from northern California (Hill 2008).

The location of this new subspecies, Neil Rock, is defined by the U.S. Geologic Survey as a "pillar" within the Cascade Volcanic Arc and it is at 42.541512° (42° 32' 29") N and 122.970326° (122° 58' 13") W in Meadows District, Jackson Co., Oregon, on the Boswell Mountain U.S.G.S. topographic map northwest of Eagle Point, 8.3 miles from Gold Hill. The peak is at 2775 feet (845 meters). Neil Rock is composed of sandstone with significant deposits of hot-springs deposited cinnabar, a source of mercury (Wiley & Hladky 1992). According to the Jackson County area soil survey (Johnson 1994) the area is in the McMullin Rock outcrop complex, with 35–60 percent slopes. The McMullin soil is formed in colluvium derived from igneous and metamorphic rock. While most

populations of *Sidalcea hickmanii* are found in areas with serpentine (Hill 2008, 2012), there appears to be no serpentine associated with this new subspecies. The site is known to have occasional fires (the last apparently in 1994) and these appear to greatly benefit the population by stimulating seeds in the seed bank to germinate and to eliminate competition from other plants, especially woody ones, as in the case of the other *S. hickmanii* subspecies (Hill 2008).

According to Wineteer (pers. comm.), the site was surveyed by botanical consultant Richard Callagan in 1992 and there was no sign of *Sidalcea* at that time. In 1994 there was a large forest fire on and around Neil Rock (the Hull Mountain Fire) and in May 1995 the *Sidalcea* was first seen by Callagan. In May and July 1997 Callagan again visited the site and recorded more than 500 individuals of this plant, 90% of which were mature. On 22 May the plants were in bud with several in flower, on 6 July the plants were fruiting. In 1998 Wineteer visited the site and vouchered this population. Wineteer and Callagan again visited the site in 2003 and collected additional material and recorded their observations. Several additional site visits have been made since that time.

Halse traveled to Neil Rock on 11 Jun 2009 to study the plant and to collect more specimens (Figs. 1–4). The population was noted to be gynodioecious by Halse. There were both bisexual-flowered plants and pistillate-flowered plants. A few were starting to set seed and these all seemed to be the pistillate plants. Bisexual-flowered plants may or may not have been successfully forming seeds because they were immature. Both plant types were visited by pollinators that included 28 insect species in 6 orders (Schroeder et al. 2012). The most numerous were Hymenoptera dominated by Megachilidae, including *Hoplitis* and *Osmia*, and Coleoptera, including *Anthonomus* (Curculionidae) and *Trichodes* (Cleridae). The vast majority of the plants had white flowers (Figs. 1, 2, 4). One or two of the pistillate plants with reduced petals had pink or pale pink flowers (Fig. 3). Specimens from this gathering have been chosen as the type specimens.

Sidalcea hickmanii Greene subsp. **petraea** S.R. Hill & R. Halse, **subsp. nov.** Figures 1–4. **TYPE: USA. Oregon**. Jackson Co.: Top of Neil Rock, ca. 14 air mi NNW of Medford, elev. 845 m, N 42.54145° W 122.96996° WGS84, shallow soils over rock, W-facing slope; plants perennial, flowers white, bisexual; associated taxa *Ceanothus*, *Quercus*, *Pinus*, *Arctostaphylos*, *Toxicodendron*, *Clarkia*, *Eriophyllum*, 11 Jun 2009, *R. Halse 7644* (holotype: OSC 242200 [Fig. 1]; isotypes: CAS, GH, ILLS, MO, NY, WTU).

The white flowers (rare in *Sidalcea*) of subsp. *petraea* in congested spicate racemes terminating several branches per stem are somewhat reminiscent of *Sidalcea malachroides* (Hook. & Arn.) A. Gray. Vegetatively it most closely resembles subsp. *parishii* (B.L. Rob.) C.L. Hitchc. but can be distinguished from that by its predominantly 2 rather than 3 bractlets, its predominantly white flowers, and its geographic range. In addition, it and subsp. *anomala* are the only subspecies that produce both pistillate and bisexual flowers so far as is known.

Herb, perennial, (0.3–)0.5(–0.9) m tall, finely stellate pubescent (some parts ciliate, and minute simple hairs sometimes present), stellate hairs 0.1–1.0 mm in diameter, 2–5-rayed, with woody caudex and taproot. **Stems** few to many, clustered, often tinted pale brick-red proximally, simple or 2–10-branched above, erect, not hollow (pithy). **Leaves**: cauline; stipules on main stems 4–6 mm x 1.5–2.5 mm, falcate, ovate to lanceolate, acute to obtuse, gen. 3-veined, ciliate and puberulent; proximal petioles (3.5–)5.0–6.5(–9) cm long, distal shorter, (0.5–)1–2(–3.2) cm long, finely stellate-pubescent, 1/2 to 3 times as long as blade, shortest on distal-most leaves; blades not lobed, all similar in shape, nearly equal in size except for distal-most which are gradually reduced, crenate-dentate, usually flabelliform or reniform, rounded at apex, base wide cuneate, truncate, to wide-cordate, generally wider than long, proximal (2.0–)3–4.5 cm long x (2.3–)3.0–5.5 cm wide, distal blades 2.1–3.5 cm long x 3.0–5.0 cm wide, stellate-pubescent, hairs 2–3(–4)-rayed, mostly on veinlets, generally not overlapping, sparser on adaxial surface. **Inflorescences** terminal spicate

racemes, each simple and not or little elongating in age, (1.5–)3.5–5.0(–7.5) cm long (excluding peduncle, if present), flowers usually congested, proximal-most sometimes solitary axillary, calyces overlapping at least distally and in bud; axis densely stellate-pubescent; bracts 5.0–6.0(–8.0) mm long x 1.0–1.5 mm wide, about (1–)2 times longer than pedicels and slightly shorter than calyx, narrowly lanceolate to oblanceolate, 1–3-nerved, persistent, finely stellate-puberulent, ciliate, 1–2, paired or bifurcate to simple (i.e., bracts fused); involucellar bractlets 2 (rarely 3), linear to narrowly lanceolate, 4.0–5.0 mm long x 0.2–1.0 mm wide, slightly shorter than calyx (1–2 mm shorter than sepal apices), minutely ciliate-pubescent, 1-veined. **Pedicels** 1.5–2.0 mm long, gen. not obscured by bracts. **Flowers**: bisexual or pistillate, plants gynodioecious; calyx 5–6 mm long, finely stellate pubescent, often sparsely so, lobes 2–2.5 mm x 4 mm, short-acuminate, 3 veins often visible; petals of bisexual flowers 10–11 mm x 6–7 mm wide, generally white (figs. 1, 2, 4), apex notched 1–2 mm deep; petals of female flowers smaller, white or occasionally pink (fig. 3), 6 mm x 2.5–4 mm wide; staminal column 5–6 mm, minutely stellate pubescent, anthers white; perfect flowers protandrous; stigmas 6–8. **Fruits** schizocarps ca. 5–7 mm in diameter; mericarps 6–8, each 2 mm x 2.5 mm, glabrous; margins, back corrugated-ridged, back with a medial ridge; mucro 0. **Seeds** 1.5–2 mm, glabrous. ***2n*** = ? [probably *2n* = 20].

Flowering late May–June, fruiting June–August. Shallow soil, rocky areas, outcrops; shrub community (ridge chaparral), associated taxa *Arctostaphylos, Quercus, Pinus, Toxicodendron, Ceanothus cuneatus, Calocedrus, Clarkia, Trifolium, Chondrilla, Bromus, Daucus pusillus, Eriophyllum, Chlorogalum, Cynosurus;* 845 m. Known only from Neil Rock in Jackson Co., Oregon.

Additional specimens examined. **USA. Oregon**. Jackson Co.: Top of Neil Rock, off Rock Creek Road [and Duggan Road on BLM Road 35-2-20.0], T35S, R02W, Sec. 8, 25 Jun 1998, *Wineteer s.n.* (BLMM923); top of Neil Rock, NESW Sec. 8 T35S, R2W, 13 Jun 2003, *Wineteer MW-1-061303* (BLMM2126; OSC); top of Neil Rock, ca. 14 air mi NNW of Medford, elev. 845 m, N 42.54145°, W 122.96996°, shallow soils over rock, W-facing slope, associated taxa *Ceanothus cuneatus, Arctostaphylos, Quercus, Pinus, Trifolium, Daucus pusillus, Toxicodendron,* 11 Jun 2009, *Halse 7645* (ILLS, OSC 242202, WTU), *Halse 7646* (ILLS, OSC 242203 & 242204, WTU), *Halse 7647* (ILLS, OSC 242201, WTU).

Sidalcea hickmanii subsp. *petraea* is the most northern population of the species and the only population known in Oregon. Subsp. *petraea* is known only by a single population.

Subsp. *petraea*, named after its rocky habitat, is included within *Sidalcea hickmanii* because of the congruence of the habitat, habit, leaf, bractlet, floral, and fruit characters. The subspecies of *S. hickmanii* all share the following characters: lack of basal leaves, cauline leaves that are evenly spaced and differ little in size and shape from proximal to distal portions of the stems, presence of (2–)3 involucellar bractlets, and non-cuspidate (without a cusp, mucro or 'beak') mericarps. The new subspecies differs from the others in having predominantly 2 involucellar bractlets and usually white flowers, only rarely seen in *Sidalcea* (previously known only in *S. malachroides* and *S. candida* A. Gray, rarely in individuals of *S. calycosa* M.E. Jones subsp. *calycosa,* and, perhaps, in *S. malviflora* (DC.) A. Gray subsp. *laciniata* C.L. Hitchc.).

The species *Sidalcea hickmanii* is found in small, isolated populations from southern California to southwestern Oregon and appears to have a relict distribution. Andreasen and Baldwin (2001, 2003) suggested that it is one of the basal species within the genus.

Figure 1. Holotype of *Sidalcea hickmanii* Greene subsp. *petraea*. Bisexual individual.

Figure 2. *Sidalcea hickmanii* subsp. *petraea* individual at the type locality. Typical white-flowered individual. Bisexual individual. Photo R.Halse, 11 June 2009.

Figure 3. *Sidalcea hickmanii* subsp. *petraea* at the type locality. Less frequent pink-flowered pistillate individual. Photo R.Halse, 11 June 2009.

Figure 4. *Sidalcea hickmanii* subsp. *petraea* bisexual individual at the type locality, with *Eriophyllum*. Photo R.Halse, 11 June 2009.

Key to the subspecies of *Sidalcea hickmanii*

1. Most leaf blades deeply lobed +/- to base; California.

2. Bracts (7–)10–12 mm, equaling or shorter than calyx; San Luis Obispo Co. ..... **subsp. anomala C.L. Hitchc.**
2. Bracts 5.5–7 mm, shorter than calyx; Napa Co. ..... **subsp. napensis S.R. Hill**

1. Leaf blades unlobed or deeply crenate to shallowly lobed; California, Oregon.

3. Involucellar bractlets predominantly 2; petals white to infrequently pale pink; flowers bisexual or pistillate; sw Oregon ..... **subsp. PETRAEA**
3. Involucellar bractlets 3; petals pink, pale pink, or pinkish lavender to pale lavender; flowers bisexual; California.

4. Bracts broadly lanceolate, 5–7(–10) x 2.5–4 mm, slightly shorter than calyx; involucellar bractlets equaling or slightly shorter than calyx; distal leaf blades unlobed or very shallowly lobed to 1/4 their lengths; Santa Barbara and San Bernardino cos. ..... **subsp. parishii (B.L. Rob.) C.L. Hitchc.**
4. Bracts linear, lanceolate, or oblong, 2–7 x 0.5–2 mm, shorter than calyx; involucellar bractlets shorter than calyx; distal leaf blades usually unlobed; Lake, Marin, or Monterey cos.

5. Plants 0.4–0.8 m, greenish- to grayish-canescent; calyces stellate-puberulent, marginal hairs longest; involucellar bractlets 2–7 mm; largest leaf blades deeply cordate, 2.5—7 cm wide; inflorescences dense; Monterey Co. ..... **subsp. hickmanii**
5. Plants 0.1–0.4 m, greenish, sparsely or moderately hairy; calyces stellate-puberulent, hairs uniform in length; involucellar bractlets 2–4 mm; largest leaf blades truncate to wide-cuneate, 0.7–2.7 cm wide; inflorescences open; Lake or Marin cos.

6. Bracts of distal flowers 1, cupped; leaf blades 0.6–1.5 x 0.7–2.2 cm; stems distally with appressed hairs 0.2–0.5 mm; plants 0.1–0.2(–0.4) m; inflorescences not spicate, to 10-flowered; calyces 4–5.5 mm; n Lake Co. ..... **subsp. pillsburiensis S.R. Hill**
6. Bracts of distal flowers usually 2, flat or cupped; leaf blades (1–)2–4 x (1–)2.7 cm; stems distally with tufted hairs 0.5–1.2 mm; plants (0.2–)0.3(–0.4) m; inflorescences spicate in age, 10+-flowered; calyces 6–7 mm; Marin Co. ..... **subsp. viridis C.L. Hitchc.**

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